

INSECTES SOCIAUX

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COMITÉ DE RÉDACTION

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I

MÉMOIRES ORIGINAUX

STUDIES OF CASTE DIFFERENTIATION IN MYRMICA RUBRA L. 3. LARVAL DORMANCY, WINTER SIZE AND VERNALISATION

by

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INTRODUCTION

In the previous two papers in this series (BRIAN, 1954, 1955 *a*) the growth under optimal conditions, in February, of all sizes of hibernating larvae, yielding queens, males, workers and intercastes, was described. The considerable variation in size of larvae in winter, although all in the same instar, proved to be an important primary factor in caste-potentiality: Most of the largest larvae formed queens, most of the smallest, workers, and the intermediate sizes produced all types including the males. In this contribution, the causes of these winter size differences are analysed, and the physiological changes that take place during winter in workers and in larvae, and that affect their potentiality for brood-rearing and growth respectively, are considered.

Certain aspects of this problem have been mentioned earlier (BRIAN, 1950, 1951). The largest larvae are produced in early summer, in mid-June, immediately after the "rapid" brood. (1) This was shown to be the case by weekly censuses of a colony of *M. laevinodis* NYL., a very closely related species. It has since been confirmed on wild colonies by administering neutral red (dissolved in sugar solution) for one day in mid-June. This, fed to larvae in concentrations so dilute as to be undetec-

(1) "Rapid" brood is the first to be produced from eggs in a season and has no dormant phase (BRIAN, 1951).

table, is concentrated and accumulated in the urate cells of their fat-body. When the colony was collected and examined the following winter, only the newly formed adults (from rapid brood) and the largest larvae contained the colouring.

The smaller larvae are produced from eggs laid later in the season, some being so late that they only just manage to get into the third instar as very small individuals. The growth of all larvae normally ceases about mid-October after which in the two months until mid-December [the autumnal period (1)] they lose about 25 % of their weight, through dehydration. *A priori*, it is unlikely that larvae that become dormant in July (later forming the large winter ones) and others that do so in late September (the small winter ones) would be inhibited by the same factors: and the experiments described confirm this. Inhibition, it will appear, may be due to three sets of causes: (1) those intrinsic to the individual (physiological) and causing, in customary terminology, diapause; (2) those extrinsic to the individual, but intracolony (sociological); (3) those extrinsic to the individual and to the colony (ecological). These may of course interact.

DORMANCY AND THE WINTER POPULATION

In this section the conditions that govern the two alternatives that face a young larva (active growth and metamorphosis on the one hand, and dormancy on the other) are considered. It is also concerned with the character of dormancy in different size groups of larvae, and the conditions under which larvae may change from one group to another. In addition, some light is thrown on the nature of their diapause, which in most respects resembles that of other insects (as described by ANDREWARTHA, 1952).

METHOD.

In mid-September, the mean temperature of the environment is in the order of 12°-15° C and larval growth, although continuing, is at a very low ebb. By raising the temperature of groups of workers and larvae to 20° C, larval growth may be increased and metamorphosis may even take place, but the response varies very much from colony to colony.—Some, even at 25° C, will not produce prepupae, others will not even show larval growth at 20° C; alternating 12-hourly periods of 25° C and 10° C have intermediate actions.

In these serotinal incubations queens have never resulted even from large larvae and it is clear that a physiological difference must exist either in the larvae or in the workers or both and that this disappears during the winter (before February). In order to distinguish hibernation changes in workers from those in larvae it is necessary to culture the latter in September not only with workers of their own seasonal type, but with vernal workers (2), for other work (unpublished) has shown that workers vary

(1) The six season terminology is used: serotinal = mid-August to mid-October; autumnal = mid-October to mid-December; hiemal = mid-December to mid-February; and so on for prevernal, vernal and aestival.

(2) That is, workers after hibernation and three weeks culture under optimal conditions, as defined in BRIAN 1954, page 103.

seasonally in their brood-rearing performance. When cultured with vernal workers, serotinal larvae are directly comparable with larvae as usually cultured (with similar workers) in spring.

To produce these vernal workers in autumn it is necessary to take the rather drastic step of extending their winter into and through the following summer, by continuing low temperatures. This is successful provided they are kept clean. Such will, on reincubation as late as October, rear their own larvae in a normal spring manner and with similar success. Although not essential, it is easier to construct these mixtures of different seasonal types by taking larvae and workers from different nests, a procedure which introduces another element of variability into the cultures. To compensate for this, cultures homogeneous for seasonal type have also been built up with larvae and workers from different nests, a precaution which is probably unnecessary for existing evidence shows that the recognition of differences between colonies only appears with the adult stage.

In the first experiment to be described, the larvae were taken from the field in mid-September and divided into three size groups: small (average weight 0.63 mg), medium (average weight 1.65 mg) and large (average weight 2.63 mg). Each group was cultured as already mentioned with either serotinal or vernal workers at either 20° C or 25° C constant. There were thus 12 treatments composed of three variations of larval size, two of worker type, and two of temperature. Periodically, records of weight and maturity were taken and the results are presented in Tables 1 and 2 and will be considered in the next four sub-sections that deal separately with each combination of worker type and temperature level.

Vernal workers at 25° C (V 25).

In this treatment the small larvae grew immediately, so that after two weeks 16/20 reached the segmentation (B) stage of development and some were even pupae (Table 1). All were pupae after four weeks (1).

By contrast with the small larvae, the medium produced only 7/21 of such "metamorphosis guaranteed" brood after two weeks, 9 after four weeks and 11 after six weeks, and the residual larvae persisted with little change for another seven weeks (that is until the thirteenth week) when the experiment was discontinued. Thus about half this group were refractory to worker action, and even less than half responded immediately in the manner of the small larvae. It might be expected in continuation of this trend that all the large larvae would be refractory, but the contrary was the case, for 13/20 were committed to metamorphose (had passed into or beyond the B period) after two weeks. However, this only rose to 15/20 by four weeks leaving a residue of 5 refractory larvae which persisted unchanged as far as the thirteenth week after which observations ceased.

These residual larvae showed slightly higher average weights than the starting group and it is likely that the individuals had grown slightly: although the possibility that the smallest had metamorphosed cannot be excluded. The residual medium larvae averaged 2.0 mg instead of 1.7 mg and the residual large larvae averaged 2.9 mg instead of 2.6 mg.

(1) Importance is attached to the B period of larval life, explained in BRIAN 1954, because its attainment is a guarantee of early metamorphosis even in conditions of starvation; all prolonged arrests of growth and development (lasting months even) take place in the A period of the third instar, between the stages brain 0.5 to 0.8 approximately.

TABLE 1. — The numbers of larvae in the B period and beyond, and the average weight (mg) of adults ultimately produced when cultured by combinations of 2 worker types at 2 temperatures for 2 and for 4 weeks; larvae grouped according to size.

Worker type

Temperature.	Incubation period.	VERNAL.			SEROTINAL.		
		Larval size.			Larval size.		
		Small.	Medium.	Large.	Small.	Medium.	Large.
25	2	16	7	13	0	0	0
	4	20	9	15	1	2	5
Total number.		20	21	20	20	19	21
Average weight of adults.		4.0	4.0	4.8	3.7	3.8	4.5
20	2	11	7	4	0	0	0
	4	11	7	5	0	0	0
Total number.		17	21	20	24	21	34
Average weight of adults.		3.2	4.5	4.3	—	—	—

With vernal workers (pooling 20° and 25° C groups) the differences in the proportion of metamorphosing and refractory larvae within the size classes have, from the χ^2 test a probability less than 0.001.

The brain positions ranged from 0.5 to 0.8, being more advanced in the larger individuals. As this combination, vernal workers and 25° C, is the most potent growth and metamorphosing influence known, it is reasonable to conclude that the residual larvae were in diapause. This evidently is more strongly implanted in medium than in large ones.

TABLE 2. — Summary of the results of the October culture of larvae (3 size classes) in the 4 combinations of 2 temperatures and 2 worker types.

	SMALL.	MEDIUM.	LARGE.
V 25	All : g, m	Half : g, m Half : g to L	Most : g, m Few : s
V 20	Most : g, m Few : g to L	Few : g, m Most : g to L	Few : g, m Most : s
S 25	All : g to d, then m	Few : g, m Most : s	Few : g, m Most : s
S 20	Most : g to d Few : s	All : s	All : s

V = vernal, S = serotinal, 25 = 25° C, 20 = 20° C, g = grew; m = metamorphosed, s = remained static, L = large larvae, d = diapause.

Moreover, as the results of this and of other treatments show that growth from medium to large may occur (under certain circumstances) it must be assumed that this is accompanied by a (perhaps gradual) decrease in the strength of diapause.

Diapause, then, may provisionally be supposed to involve slow growth from medium larvae to large larvae with accompanying brain movement from about 0.5 to 0.8.

None of the adults were queens as they would certainly have been (from the larger larvae) in spring. The workers were larger from the large larvae (4.8 mg average) than from the medium and small (both 4.0 mg average)—Table 2. It might be concluded that the large larvae had, prior to the start of the experiment, gained stature (1) whereas the responsive group of medium larvae were merely slightly larger and more mature "small" larvae.

These observations are more easily understood with the aid of the diagram (fig. 1) constructed with an ordinate of log weight and an abscissa of the standard maturity series

(that given by February queens of the set called Q in BRIAN (1955 *a*)). Whilst the average weights of larvae and their maturity at various times, and the average weights of prepupae produced after defecation, are



Fig. 1. — Paths of larvae cultured in autumn under 4 treatments: V25, V20, S25, S20, explained in text. Larvae were initially of 3 sizes and the mean of their initial distribution is marked (open circle) except in the case of the smallest which start off the diagram. Growth may lead to "permanent" dormancy in sizes up to a limit (black circle), or to "temporary" dormancy (a cross) followed by further growth, or directly to metamorphosis (D). The path of February cultured queens (Q set) is given as a guide (thick line); other paths are largely interpolated. Ordinate: weight (mg.) on log scale; abscissa: standard maturity series.

(1) As in earlier papers the word *stature* is used in size comparisons between individuals of identical maturity.

correctly indicated, the paths (1) have been interpolated and are largely schematic. The paths of small larvae that grew and metamorphosed without break (V 25, V 20) are particularly speculative as they have been drawn going up to the "medium" state before deflecting. The justification for this is that the same type of larva in spring has been shown to behave similarly (the *a* and *b* workers BRIAN, 1955 *a*). Moreover, the paths of such in October as well as of large larvae have been studied and will be described later in this paper, and they do not differ materially from the interpolated paths of this diagram.

Serotinal workers at 25° C (S 25).

The contrast between the action of these workers and the action of the vernal workers is astonishing. After two weeks, none, and, after four weeks, only one of the 20 small larvae had passed beyond the A stage of development whereas all those under the influence of the vernal workers had pupated by this time. This does not mean that they were entirely refractory, for 18 of the 19 residuals had grown before halting at the stage brain 0.5 with an average weight of 1.8 mg. That is to say, they had entered diapause at the stage of suspected onset instead of passing on to the second half of the A period and so to the B period. This difference in the action of these worker types has been confirmed in experiments starting with eggs laid in summer (WEIR, unpublished).

However, diapause was not long lasting at this temperature, and in period four to six weeks, all but 4 passed into the B period and started to metamorphose. The average weight of adults so produced was only slightly less than that of the directly growing brood treated by vernal workers: 3.7 mg instead of 4.0 mg (Table 1), no advantage in size having been gained through the (perhaps too brief) period in diapause (2). Other work on diapause has confirmed that its duration varies considerably even in constant environmental conditions.

The medium larvae under this worker and temperature régime were even more refractory than with the vernal workers, only 2/19 being on the way to metamorphosis after four weeks. The residual larvae with an average weight of 1.8 mg and at a developmental stage of brain 0.5 (that is identical with the diapause stage of the initially small larvae) changed very little if at all. But in the next two weeks, an additional 10 passed from the A period stage leaving only 7 (3).

(1) *Path* was defined in BRIAN (1955 *a*): it is the line traced on a graph of log weight/standard maturity series by an individual or set of individuals (averaged) as they change in time (in these respects). It expresses the value of the ratio: growth rate/development rate.

(2) It is possible that the vernal cultured small larvae at 25° C pass along this same path without halting at the stage brain 0.5. In the figure (fig. 4) they have been indicated as smaller at this stage.

(3) It is noticeable that with both small and medium larvae, an increase in metamorphosis rate took place in the weeks 4 to 6. This may be due to a maturing of the worker population rather

The large larvae produced no pupae in the first two weeks and 5 in the period two to four weeks, leaving an unchanged residue of 16 larvae of average weight 2.6 mg and brain position 0.6 to 0.7. The average weight of the (all worker) adults was 4.5 mg, again slightly less than the average weight of similar progeny produced by vernal workers. From Table 1 it can be noted that all size groups of larvae yielded slightly smaller adults with serotinal workers (at 25° C). Adults derived from large larvae were about 0.8 mg larger than those from the medium and small groups which, as with vernal workers, did not differ materially.

These results and those of the previous section are thus consistent: they show the same differences in larval reaction but at a generally lower level of activity caused by the late-season character of the worker population.

Vernal workers at 20° C (V 20).

The drop in temperature of 5° C does not in any way simulate a change in worker type from vernal to serotinal, so that the differences in performance cannot arise solely from differences in activity thresholds. Thus the 17 small larvae gave a total of 11 entering the B period and metamorphosing in the first two weeks with no further additions in the second two weeks, a process resembling the behaviour of these larvae at 25° C with vernal but not serotinal workers; 6 residual larvae reached the stage brain 0.5 and there entered diapause at an average weight of 2.3 mg—large for this stage. Two weeks later they ranged from 2.0 mg (brain 0.5) to 3.2 mg (brain 0.8) and this arrangement lasted at least as long as the 13th week. At the lower temperature then, the vernal workers produced a proportion of rapid brood (as at 25° C), but, in addition, some dormant brood, and this shows the interesting characteristic of growing and developing very slowly beyond the stage of diapause onset (brain 0.5) so as to produce larvae apparently identical with the "large" winter ones. This culture may therefore be simulating the natural process whereby rapid brood is followed by the production of the large dormant larvae that overwinter. These larvae are, in fact, moving along the queen-path at very slow rates (for the path of most workers diverges before this stage—that of the *a* and *b* types at brain 0.6). Diapause then is more complex than was earlier supposed: it may now be conceived as consisting of an arrest of growth and development at the stage brain 0.5 (now conveniently called "primary" diapause), which is followed after a variable period by either quick growth and development along the worker path ending in metamorphosis, or ("secondary" diapause) slow growth and development along the queen path. In the latter case, it is in the nature of a resistance inserted in the path.

than a change in larval physiology, for it will be shown in the next section of this paper that they can recuperate from their autumnal condition at culture temperature. To avoid this complication, relays of workers should have been used; however, only the first four weeks are used as a basis for drawing any important conclusions.

The medium larvae under this treatment do not differ in any important respect from the same at 25° C. A third of them metamorphosed in the first two weeks, and the rest grew slowly into "large" larvae (along the queen path) so that after six weeks they averaged 2.1 mg and ranged from 1.7 mg (brain 0.5) to 3.1 mg (brain 0.7). The large larvae show greater stability at 20° C than at 25° C: only 4 after two weeks and 5 after four weeks had entered the B period and metamorphosed (compared with corresponding figures of 13 and 15 at 25° C). The residue show only a slight increase in average weight: from 2.6 mg to 2.7 mg ranging between 2.4 mg (brain 0.6) and 3.2 mg (brain 0.8). This is evidently the limit of growth without subsequent metamorphosis.

The adult size offers some peculiarities in this set. Those from large larvae are 0.5 mg less than at 25° C; those from small are 0.8 mg less, but those from medium are 0.5 mg more. These figures may not be significant but one might suppose that at this temperature they behaved as "large" larvae, and took the queen path up to the end of the A period (fig. 1), whereas at the higher temperature they behaved as "small" larvae and took the worker (*a* or *b*) path. This then is the second occasion at this temperature (20° C) that larvae have taken the queen path: first the small ones (that did not metamorphose), then the medium ones (both those that did and did not metamorphose).

The lower temperature evidently increases the chance of effecting a high g/d ratio and of maintaining it, especially in the relatively reactive small larvae.

Serotinal workers at 20° C (S 20).

Finally, the combination of low temperature with late-season workers can be examined. From the table it is seen that of 79 larvae in all, none metamorphosed. Thirty-two large larvae actually lost 0.1 mg of average weight (a value within the weighing error). They dropped to 2.5 mg but retained their brain position of 0.6 or 0.7. After six weeks these ranged from 2.1 mg (brain 0.5) to 3.1 mg (brain 0.6). The medium larvae were similarly unchanged and ranged at six weeks from 1.2 mg (brain 0.5) to 2.0 mg (brain also 0.5) with an average of 1.6 mg. But whereas these two groups were absolutely stable under these conditions—which were in fact nearer than any to natural ones in October—the small larvae were not. They grew substantially but they did not metamorphose. Beginning at 0.6 mg, 21 of them averaged 1.5 mg (brain 0.5) and 3 averaged 0.8 mg (brain 0.1) after four weeks. Thus the majority grew to the stage brain 0.5 and then halted (diapause?) but at a size smaller on the average than any others at this stage. From here one might envisage them behaving as medium larvae if they were treated with vernal workers, part growing with slight development into "large" larvae, and part growing and developing actively into workers after a short delay.

GENERAL CONCLUSIONS.

Considering first the small larvae under different treatments: they responded in all cases and, hence, in autumn are inhibited by low temperatures only (ecological dormancy). But they responded very variously (Table 2): at S 20 they produced diapausing "medium" larvae, so that one may conclude that the medium larvae of winter are produced in like manner: at S 25 they also produced medium larvae but these remained in diapause only briefly, later developing into workers comparable in size with the *a* types of normal spring culture; this instability is characteristic of diapause at 25° C. At V 20, the majority grew and metamorphosed immediately as did all at V 25, and although the information is not available it is reasonable to suppose that they followed the general path up to brain 0.5 and then deflected along a path similar to that followed by the *a* type workers of spring culture for they ended up with very similar weights (fig. 1). V 20 is of particular interest as it produced "large" larvae in diapause growth along the queen path. So these small larvae have under different worker treatments (at 20° C) produced the whole range of larval size-group types encountered in winter, and they have done it in a way which reproduces the seasonal cycle: if V 20 (giving rapid and large brood) is followed by S 20 (giving medium) and then, say, by S 10 (giving small). They are plastic material whose fate is fashioned by varying influences of worker type and temperature.

The large larvae are by comparison inert except at V 25 when they develop quickly into large workers. They appear to have reached the limit of diapause growth from which the only escape is into metamorphosis. The medium larvae are also inert, but some grow into large larvae under the influence of vernal workers. Thus the results give a consistent picture of the growth pattern and its governing factors which may be briefly summarised as follows.

Larvae entering the third instar (at varying sizes which are a function of various precedent conditions) grow in a manner determined in part at least by the character of the worker population and the prevailing temperature (to these can be added interlarval competition—BRIAN, 1955 *b*—and food supply and other factors). To use a morphogenetic analogy, they are meristematic material which is differentiated under the influence of the adult tissues whose action is to some extent temperature dependent. The first critical stage in the third instar is reached under all social conditions given adequate temperatures (brain 0.5); it is reached at sizes that vary at least from 1.2 to 2.3 mg and are a function of worker type, being greatest under V 20 conditions, least under S 20 conditions and intermediate under S 25 conditions. It is a stage of quiescence of varying duration (primary diapause).

The size at this stage, as well as the worker type, influences the next step which is either into a growth which leads without pause into

metamorphosis (given food: in its absence metamorphosis only takes place if the individual has reached the B period of development) or into a slow growth up to another higher limit, less clearly defined, but still in the A period at about brain 0.8. The first alternative is characterised by a low g/d ratio and gives (invariably) worker imagos, the latter by a high g/d ratio which takes the larva very slowly along the path towards queenness (but not right there without vernalisation as is later explained). As it passes along this path its stability is slowly reduced and it is more easily diverted by V 25 conditions to give worker imagines after a short period of quick low g/d growth. Movement along the path is favoured by V 20 conditions (although V 25 acting on medium larvae can do the same). The limited stability of the path is well shown by this, for, whilst vernal workers are essential, if the temperature is too high there is a marked risk of displacement. The precariousness of the queen path especially in the A period was shown to affect post-winter conditions in the previous paper in this series (BRIAN, 1955 a).

Diapause and Queen formation.

No strict association between diapause experience and queen potentiality exists, in spite of the fact that large larvae that have diapaused are the principal queen formers in spring. For a small proportion of queens are formed from larvae classed as small (albeit the larger of these) that have not reached by winter the stage brain 0.5. These are, of course, the *q* set.

Diapause then must be regarded as a brake applied to the growth of larvae in summer that has the effect of conserving them until the following spring. During their phase of diapause growth they accumulate protein reserves in their trophocytes, as is shown by the presence of abundant eosinophil granules in their cytoplasm. This increase in volume of the fat-body is accompanied by an increase in girth rather than of length; in fact the phase of growth up to brain 0.5 is characterised by elongation and construction of the body framework, whilst that after is one of filling out. By comparison, larvae in the pre-brain 0.5 state have smaller trophocytes which lack protein granules in the cytoplasm.

The necessity for this brake is related to the character of the brood-rearing system of the species which is probably one of its principal adaptations to life in (for ants in general) a microthermal climate (BRIAN, 1951). For, unlike other species (of *Formica* for example), the *Myrmica* require quite high temperatures (comparable with those of the tropical *Ecophylla longinoda* LATR.—vide LEDOUX, 1950) for oviposition and metamorphosis. Whilst they achieve this partly by constructing their nests as, and in, heat traps, their chances of survival must be further enhanced by their partial 2-year brood cycle, which allows larval growth, the process with the lowest temperature threshold, to continue in the cool spring and autumn months. In addition, the chances of success in the nuptial

flight must obviously be maximised, and as there appears to be little doubt that the times of year used (July and August) are climatically most suitable, it is evidently an advantage to produce sexuals and to mature them as early in the summer as possible so that the most use can be made of the few climatically optimal days. Hence the retardation of larvae in the warmest part of the year by diapause at a stage which appears to be as near as possible to one in which metamorphosis is inevitable (assuming that pupae and winged sexual adults do not hibernate successfully).

VERNALISATION

THE RELEVANT PHYSICAL FACTORS.

In none of the autumn cultures discussed, nor, indeed, in any culture at that time of year, have queens resulted even from the largest larvae. In searching for the factors that bring about the change in winter, a number have been tried. Dehydration, which certainly occurs naturally, has proved ineffective at ordinary temperatures. It is possible that deep in the soil (perhaps even locked in by water) the atmosphere becomes charged with carbon dioxide and short of oxygen in winter, but experimental confirmation of the vernalising activity of such gas mixtures has not been forthcoming. Even entirely artificial stimuli such as ether, nitrous oxide, wounding, extreme temperatures and others have given no positive result.

It is evident, therefore, that the prolonged sub-growth or sub-metamorphosis temperatures normally encountered during winter are the most likely vernalising influences. In an experiment on this subject, large larvae were given four treatments in mid-August, at the hottest part of the year. They were either put at 3° C constant following a gradual fall lasting several days, or at 20° C constant; or at an alternation: half 25° C, half 10° C; or at natural, but lagged temperatures slowly falling from an average about 15° C to an average about 11° C. After two months there had been no change at 3° C; at 20° C and at natural temperature (hereafter abbreviated to NT) weight had been lost but only 0.35 mg and 0.6 mg respectively per average individual; and at the alternating temperature worker pupae had been produced indicating that this temperature was equivalent to 25° C in its action. The three remaining cultures were then treated as follows: the 20° C set were put at 3° C and after two months (four from the start of the experiment) all were incubated at 25° C. One group had thus had four months at 3° C, one had had two months at 20° C and two months at 3° C, and one had had four months of natural temperatures.

The yields were as follows: constant 3° C gave 9 queens and 1 worker; NT gave 8 queens and 2 workers; and the half 20° C half 3° C gave only 1 queen and 3 workers with 6 workers that died in the act of ecdysing

into pupae. Hence in mid-August large larvae were ready for winter, and prolongation of summer temperatures is unnecessary from their point of view—an observation which accentuates the remarks of the previous section concerning the function of diapause. Other larvae can, of course, be added to their ranks. Further, constant temperature near freezing (and well below growth threshold) and the higher irregular temperature near the growth threshold seem to confer queen potentiality equally well.

To further examine the effects of temperature régime on workers and larvae separately, four colonies were collected in September (each forming a replicate) and split into three parts kept severally at 3° C constant, at NT and at 20° C constant. The NT régime is in the order of 12 to 15° C at that time of year in mid-west Scotland, and this thus represents a fluctuating irregular temperature between the other two. After six weeks treatment, the workers and larvae of each replicate were separated and regrouped in all the nine possible combinations: 3 larval pre-treatments, times 3 worker pre-treatments. All were then cultured optimally at 25° C.

A week later it was clear that all cultures with larvae that had been pre-treated at 20° C were producing prepupae, whereas none of the others were, although their larvae were growing. The 20° C régime had permitted larval growth in all four replicates (and in three even a little metamorphosis had taken place).

After three weeks, all cultures had metamorphosed all brood, and this was sorted into workers, males and queens, counted and weighed. No differences were apparent between the 4 colonies (replicates) and these have therefore been pooled to simplify tabulation (Table 3), but in statistical tests they have of course been used together with the interactions involving them, to calculate error variance. Thus the 4 colonies and the 9 treatment combinations gave in all 35 degrees of freedom, divisible into 2 for worker pretreatment differences, 2 for larval differences, and 4 for their interactions, leaving a remainder of 27 for error.

Only larvae that had been subjected to the two lower temperatures produced queens (1); statistical analysis is unnecessary in such a case. Rather more queens came from NT cultures than from 3° C ones but this difference is not significant (by χ^2 P: 0.05-0.10). Differences in worker pre-treatment appear to have no effect. Analysis of variance of the average weights of the workers produced shows that the differences due to larval pre-treatment are significant ($P < 0.001$) but no others. Thus the general conclusion emerges that, whilst workers are unaffected by a wide variation in temperature régime, the larvae only acquire queen potentiality (under subsequent normal growth conditions) at NT and at 3° C, in itself quite a wide range (3-15° C) to show no differences. It seems quite likely therefore that an unspecific sub-growth temperature

(1) The six weeks period was of course short compared to the winter they normally experience.

is the main prerequisite for larval vernalisation. Further, only a short period is needed (6 weeks, and perhaps less) for its action, much less than must normally be received. No experiments have been directed to the discovery of the exact nature of the temperature/exposure relation.

TABLE 3. — The numbers of workers, queens and males, and the average weight (mg) of the workers (only) produced when larvae and workers, pretreated in 3 different temperature regimes, are brought together and cultured in all combinations.

WORKER pretreatment.	ADULT FORM and worker weight.	LARVAL PRETREATMENT.			
		20° C.	NT.	3° C.	Sum.
20° C	Queens.	0	6	6	12
	Males.	1	1	3	5
	Workers.	22	20	18	60
	Weight.	3.2	4.2	4.1	11.5
NT	Queens.	0	9	5	14
	Males.	0	2	3	5
	Workers.	20	16	30	66
	Weight.	3.2	4.1	3.9	11.2
3° C	Queens.	0	9	5	14
	Males.	2	1	2	5
	Workers.	27	20	24	71
	Weight.	3.6	4.1	4.9	12.6
Sum	Queens.	0	24	16	40
	Males.	3	4	8	15
	Workers.	69	56	72	197
	Weight.	10.0	12.4	12.9	35.3

NT = natural temperature.

Weight = Average weight (mg) of workers (only).

As no difference in performance between the workers could be detected, it must be presumed that the change in the worker population during the winter is largely temperature independant, a result which requires further study. The action may be a normal maturation process that brings the young of the previous summer into a ripe condition for nursing, or it may be a physiological recuperation affecting all age groups alike.

October ontogenies.

The remainder of this paper is concerned with the study of the ontogenies of singly cultured individuals which may be compared with those of February-cultured material already described in detail (BRIAN, 1954.

1955 a). The larvae were obtained from the field and were cultured with specially produced vernal workers at 25° C.

(a) *Large female larvae*. — In the middle of October, 20 ontogenies of this type were followed. Initially the larvae weighed 2.2 to 3.4 mg and ranged in maturity from brain position 0.4 to 0.6. Unlike vernal culture, growth was never resumed immediately: thus in the first four days no larva gained more than 0.5 mg: yet 13/20 had gained more than this by the eighth day. The total duration from start to finish (that is, to defecation) was as a result often long and variable. The actual figures were (in days): 8, 9, 11, 12 ($\times 4$), 13, 14, 15 ($\times 2$), 16, 17, 18, 20, 24 ($\times 3$), 27 and 29.

TABLE 4. — Summary of the ontogenies of large larvae cultured by vernal workers in October, forming workers.

PERIOD.	MATURITY.			WEIGHT.			WING AREA (1).			NUMBER of Larvae.
	Min.	Mean.	Max.	Min.	Mean.	Max.	Min.	Mean.	Max.	
C	d	d	d	3.4	4.4	5.3	—	—	—	19
	e	e	e	3.9	4.9	6.0	—	—	—	19
B	2	3	t	3.6	4.6	5.5	3	3.6	4	19
	1	2	3	2.9	4.0	5.0	3	3.6	4	19
	1	1	2	1.9	3.6	4.5	2	3.3	4	19
A	0.6	0.8	1.0	1.9	3.3	4.3	2	3.0	4	19
	0.4	0.7	1.0	1.9	3.0	4.1	2	2.6	3	19
	0.4	0.6	0.9	2.0	2.9	4.0	2	2.5	3	19
	—	—	—	—	—	—	—	—	—	19
	—	—	—	—	—	—	—	—	—	19
	—	—	—	—	—	—	—	—	—	18
	0.4	0.6	0.8	2.1	2.7	3.4	2	2.0	2	18
	—	—	—	—	—	—	—	—	—	17
	—	—	—	—	—	—	—	—	—	13
	—	—	—	—	—	—	—	—	—	12
	—	0.6	—	2.2	2.7	3.3	2	2.0	2	11
	—	—	—	—	—	—	—	—	—	9
	—	—	—	—	—	—	—	—	—	7
	—	—	—	—	—	—	—	—	—	6
	0.4	0.6	0.8	2.2	2.7	3.4	2	2.0	2	6

(1) Wing area has been measured in micrometer units that are identical with those used in previous reports in this series of publications.

However, once growth started it went on without pause (except in one case that has been treated as anomalous and considered separately) in a remarkably uniform way which permitted the calculation of means by the B-concurrence method (BRIAN, 1954, page 112). These together with the range of variation are set out in Table 4. The leg area which behaved in every way like previous cases, correlating closely with the degree of leg

segmentation, has been omitted. All progeny were typical workers as earlier defined (BRIAN, 1954, p. 108).

The C period is short, of one day in 16/19 individuals, one and a half days in 2, and two days in only 1 individual. The B period is remarkably short: 6 cases of two days, 2 of two and a half, 10 of three and 1 of four days. The mode is thus 3 days and identical with that of the *c* spring workers. The cases of 2-day B periods gave brief sequences of developmental stages as follows: 1, 3, e, d. These are the first examples so far recorded of such short segmentation periods. The A period is at first characterised by a very slow development rate then as growth starts a quick change to a high rate takes place; but this rate is no higher than that of *a* workers in the same stage. Thus these larvae are at first refractory, then they develop at rates as high as (higher in some cases) those observed in spring cultures.

The average size of this group was 4.4 mg after defecation, and they are thus between the mean size of *a* and *c*

spring types. Their specific growth rate is for the brief B period as high as that of these worker groups (fig. 2), but in the A period this is far from being the case. Their high average weight at the start is largely due to their being hydrated. The results of combining these elements can be seen in figure 3. These larvae as a group show very low g/d ratios throughout their ontogenies with the exception of a briefly sustained initial phase of higher value.

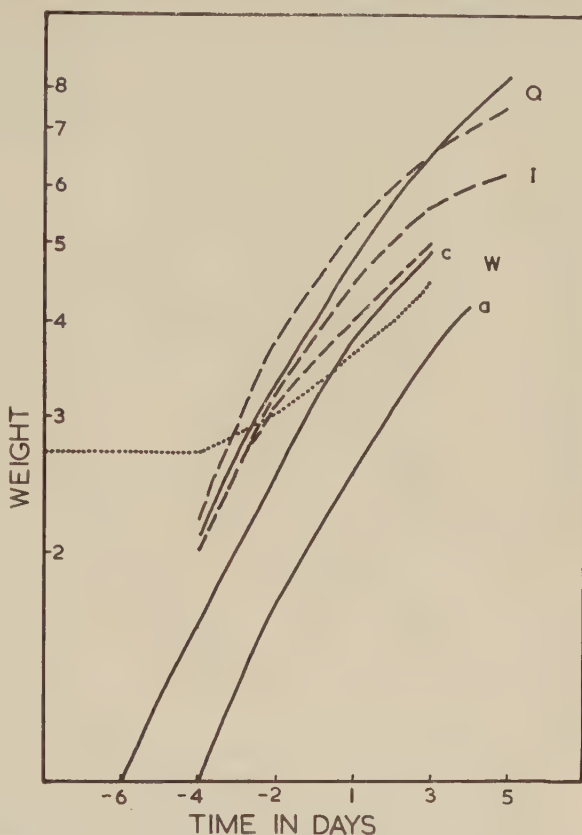


Fig. 2. — Specific growth curves from October large larvae (dotted line), from mid-winter large larvae (broken line) and from February larvae of various sizes (fullline). The October lot formed workers (W) only, the mid-winter lot formed queens (Q, top), intercastes (I, middle) and workers (W, bottom). The February curves are given as guides: the Q set (top), the *c* workers (middle) and the *a* workers (bottom). Ordinate: weight (mg.) on a log scale; abscissa: time in days measured in all cases from the start of the B period (day 1).

The wing growth measured in the same units as previously presents no peculiarities in these larvae: it is almost identical with that of *a* workers going slowly from area 2 at brain 0.6 to a maximum of nearly 4 in the B period (fig. 5).

The single anomaly of this group, spent 16 days in its initial state

(2.5 mg and brain 0.6), then in one day it rose to 3.4 mg and brain 0.8. After this it grew no more but nevertheless developed normally and even began to defecate. But in this act it died. If it had succeeded, its weight would have been in the order of 2.5 mg—an exceptionally low value.

Thus in October, with vernal workers, these large female larvae are at first unresponsive then they grow at a rate which rises to normal in the B period, whilst a slow to normal development rate in the A period is followed by a high rate in the B period. In effect, an initially queenlike g/d ratio is only briefly sustained.

(b) *Male larvae*.—Twenty male larvae were cultured in October by vernal workers. Of these, one died after 14 days without growth, and two others were apparently damaged by the workers (to judge from black scars) and they died without maturing.

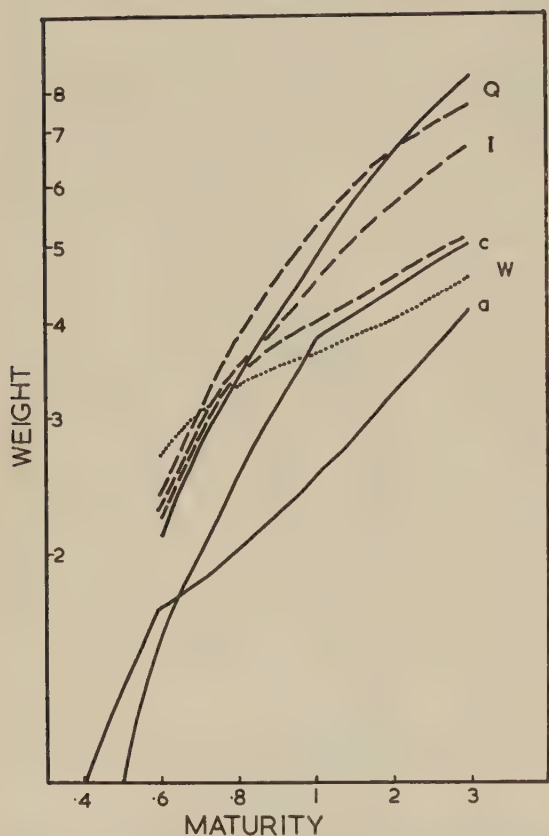


Fig. 3.—The paths of: October large larvae (dotted) forming workers (W); mid-winter large larvae (broken) forming queens (Q, top), intercastes (I) and workers (bottom); and of February larvae of various sizes (full): the Q set of queens (top), the *c* workers, and the *a* workers (bottom). Ordinate: weight (mg) on a log scale; abscissa: standard maturity series.

The details of the remaining 17 are set out in Table 5 and figured in figure 4. As the variability of the ontogenies was rather greater than with the females just described, or with the February males, coordination by the B-concurrence method was replaced by linkage at the beginning of the B period, giving a maximum congruity in the central and most important part of the maturity series. Wing growth resembled that of spring cultures and has been omitted.

The males, unlike the large female larvae, respond immediately to the action of vernal workers, that is they are not in diapause. The A period averages about 6 days as with the February cultured set and is characterised by a very slow change of brain position. The duration of the B period is more variable: 4, 5, 6, 7 and 8 days were taken by 7, 7, 1, 1 and 1 individuals. Thus the 4-day period, so rare in spring (1 out of 23), was as common as the characteristic 5-day period. In this respect then, there is a slight suggestion of similarity with the females (in which the B period

TABLE 5. — Summary of the ontogenies of male larvae cultured by vernal workers in October.

PERIOD.	MATURITY.			WEIGHT.			NUMBER of larvae.	STANDARD maturity series.	AVERAGE weight.
	Min.	Mean.	Max.	Min.	Mean.	Max.			
C	d	d	d	3.5	5.7	7.2	14	d	5.7
	e	e	e	4.8	6.4	7.5	14	e	6.4
B	2 1/2	2.6	t	4.4	5.8	7.9	14	t	6.4
	2	2.5	3	4.5	5.3	6.4	14	3	5.6
	1 1/2	1.9	2 1/2	4.3	4.8	5.7	14	2 1/2	5.3
	1	1.5	2	3.1	4.3	5.2	14	2	4.9
	0.8	1.0	1 1/2	3.1	3.6	4.5	14	1 1/2	4.3
							14	1	3.6
A	0.7	0.8	1	2.6	3.3	4.3	14	0.9	3.4
	0.6	0.8	0.9	2.4	2.9	3.7	14	0.8	3.0
	0.6	0.7	0.8	2.1	2.6	3.6	14	0.7	2.5
	0.6	0.7	0.8	2.1	2.4	3.3	14	0.6	2.3
	0.6	0.6	0.7	2.0	2.3	2.8	14	0.5	—
	0.6	0.6	0.6	1.8	2.2	2.8	14	0.4	—

The last column gives the average weight per unit of the standard maturity series which is that of February queens.

in autumn is much shorter than in spring). It is the presence of seven 4-day period individuals that causes the low maturity index value 2.6 on the last day, for these had of course passed on into the C period and could not contribute to this value, which consequently was biased by the relatively immature 6, 7 and 8 day individuals. The C period was one day in 12, and two days in 5 cases, and hence not significantly different from the spring pattern (12 of one day, and 11 of two days). Thus in the maturity series there are only slight and statistically insignificant suggestions of a shorter post-A period than in February grown males.

It is clear from figure 4 that the mean specific growth rate curves of autumn males are almost identical with the spring ones in the B period but not in the A period. This is due to the fact that the autumn ones start in a hydrated stage: at initial weights ranging from 1.8 mg to 3.3 mg instead of 0.5 mg to 1.5 mg (1) and in no case was the brain position less

(1) This is a larger difference than is encountered in females, but the reason is unknown: it may partly be sampling error.

than 0.6 in autumn. Presumably much of the earlier growth of the February males is due to rehydration, not genuine increase in body tissue. The difference in weights after defecation, of the two types, are not statistically significant ($P > 0.10$).

The g/d relation of the autumn males is reasonably constant and similar to that of the spring males after the stage brain 0.8. Prior to that the

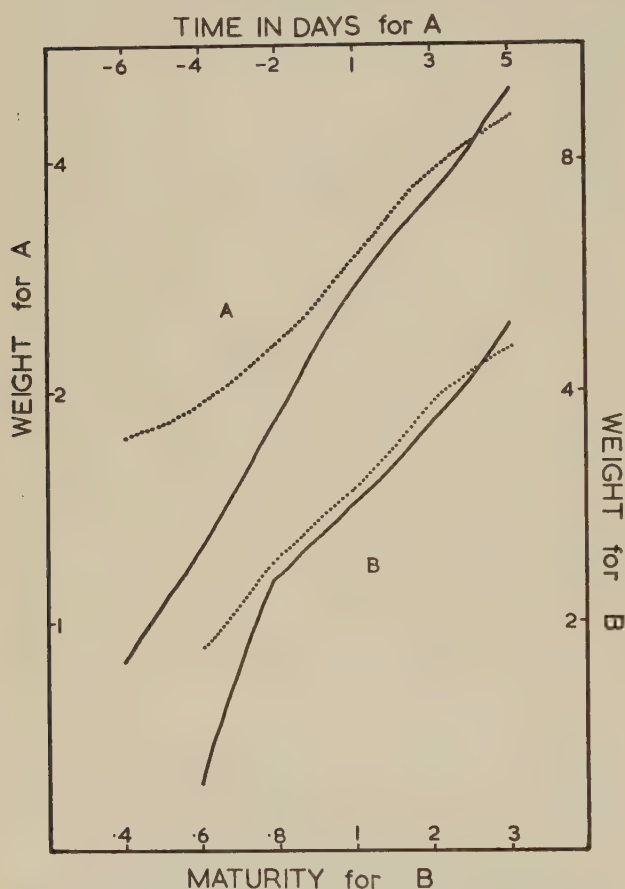


Fig. 4. — Male specific growth curves (A) and paths (B) in October (dotted) and February (full); for A, the top abscissa and left ordinate; for B, the bottom abscissa and right ordinate.

high specific growth rate of the spring set dominates their trend. Thus the conclusion is reached that the main difference in growth is traceable to differences in initial hydration. Suggestions that the B period and C periods are slightly shorter are not significant statistically. There is certainly no major change in growth potential following hibernation in males, as there is in females.

Since the males do not experience diapause, they must be produced late enough in the season to be inhibited by socio-ecological factors. Their position in the winter population size - distribution is central and well within the total female range (BRIAN, 1954, p. 118), so that this is con-

sistent and it is reasonable to conclude that they are produced after the main queen-forming set.

(c) *Small female larvae*.—In February, these produce workers for the most part, but some of the larger ones yield queens (termed in the earlier paper, the *q* set). In October, no record of queen production exists in spite of many hundreds of small larvae having been reared by specially produced vernal workers. It has already been pointed out that they

respond immediately to such (in contrast to large larvae), thereby resembling the males.

Twelve ontogenies have been studied in individual detail and they resemble in every way those of their spring counterparts, giving *a* and *b* worker types. Their B periods were of four and five days and their average weight after defecation was 3.8 mg which is not significantly different from the average of the corresponding February set: 4.0 mg. It is curious that the majority should be unaffected by vernalisation whilst a minority are markedly affected.

Mid-winter ontogenies.

Having established the fact of a striking difference in the growth potentiality of large female larvae before and after winter (October as compared with February), investigations were directed to considering the transition. For this purpose, stock colonies were collected from the field in October and stored in glass containers under 30 cm of soil so as to give as close as possible a similitude to natural climatic conditions. As a minor variant, some workers were kept in two temperature régimes in addition to the above: 2° C constant and 20° C constant. As no difference in their effects were subsequently found, no further reference to this subject is required other than to recall that the results confirm earlier findings.

Specially prepared vernal workers were not used in this set of experiments: hence worker and larva changes may be confused, but the widespread independant prior information suggests that the differences lie more with the larvae than the workers. Moreover, comparison of the actions of serotinal and vernal workers on larvae in autumn has shown that the difference is that the latter reduce the initial pre-responsive period without affecting the subsequent ontogeny.

Two sets of cultures were set, one in early December, and one in early January. Both times all possible female forms—workers, intercastes and queens—were produced, but there were more workers and intercastes in December (6 workers, 6 intercastes and 2 queens) and more queens in January (2 workers, 2 intercastes and 14 queens). Since the ontogenies of each female type were similar in whichever month they were produced, the data from the two sets of cultures has been pooled and subdivided on this (adult form) basis. Before presenting it however, it should be pointed out that the distinction has not always been easy to make, and the next section is devoted to a consideration of this.

(a) *Female classification.*—The range of variation has been so great that these adult types are to some extent arbitrarily separated; especially the division between workers and intercastes. It will be recalled that workers were defined as having: at most very small lenses in their ocelli,

no trace of wings or a suture between postnotum and mesonotum, and only one ovariole in each ovary. Individuals that do not come into either group are referred to as intercastes (BRIAN, 1954, p. 108).

One case, producing a worker by definition, was known to have a larval wing of 9 units area, which is unusually large. Other workers with larval wings of 5 and 6 units have appeared too. An intercaste with a wing of only 9 units has also occurred: it had in fact single-ovariole ovaries and was only classed as an intercaste on account of a suture, which, though not very distinct, was unmistakable. In all, 4 intercastes (out of 8 altogether) with single-ovariole ovaries have occurred in this sample, all classed as a result of thoracic or ocellar characters and all showing substantial wing development in the larva (9 to 14 units). At the other extreme one intercaste with ovaries of $8 + 8$ ovarioles but without full wings had appeared, but no cases of partial imaginal wings have been encountered. Thus most of these intermediate forms resembled workers rather than queens.

The data have not been tabulated as previously, giving the mean and range of variations of weight, wing area and maturity index day by day, partly because of the greater variability of this transition material, and partly since it has been felt that more reliance could be placed on the maturity index. Wing area and weight have been averaged per maturity unit for each female group, and their range of variation given. Specific growth rate must of course be obtained by day by day averaging after the ontogenies have been linked arbitrarily at some point—the start of the B period has been chosen for this. Maturity indices have been averaged on this time scale too, so that these may be compared with the standard (February queens) series. Again it might be stressed that grouping and averaging have only been done where the data show continuous variation and are compact. Two rather aberrant workers have been treated separately.

(b) *The workers*.—Thirty-two out of 35 larvae produced adults and of these 8 were workers, 6 from the December lot and 2 from the January lot. Two of the December lot were slightly anomalous and have been described at the end of this section. In the A period the normal sequence of maturity indices: 0.6, 0.7, 0.8, 0.9 has been acquired but in the B period the average sequence of 1.2, 2.2 and 3.0 (caused by 5 individuals with a period of three and 1 with a period of two days) is still similar to the October mode. The C period is of one day for all.

The specific growth rate of the 6 "normal" workers (Table 6 and fig. 2) is much higher in the A period than in October, perhaps partly due to rehydration. In the last two days it falls off slightly, and in the B period is identical with that of the October ones, as well as of the *c* workers from February culture. The final weight, 4.7 mg, is very close to the latter but exceeds that of the October set. The net result is that the path of these workers deflects at brain 0.8 later than the turning point of the October

ones and assumes a direction parallel to that of the other two groups (fig. 3).

The wing rises on the average to a maximum of 5 units at the 1-segment leg stage and deflects from the queen path at brain 0.8 as with the weight. However, this conceals a good deal of variation, for one worker (a January one) grew a wing of 9 units, the increase taking place even in the (2 day) B period from 7 at the end of the A period. Another worker showed a wing maximum of 6 units, two of 5 units and four of 4 units. In this

TABLE 6. — Weights and wing areas averaged per term of the standard maturity series for 6 workers produced from the mid-winter culture of large larvae; also, weights and maturity indices averaged day by day using the start of the B period as origin.

PERIOD.	STANDARD maturity series.	WEIGHT.			WING AREA.			DAYS from origin.	DAILY mean weight.	DAILY mean maturity.
		Min.	Mean.	Max.	Min.	Mean.	Max.			
C	d	4.4	4.7	4.9	—	—	—			
	e	4.7	5.1	5.4	—	—	—			
	t	—	—	—	—	—	—			
B	3	4.4	5.1	5.5	4	5	9			
	2 ½	—	—	—	—	—	—			
	2	3.7	4.6	5.0	4	5	8	3	5.1	3.0
	1 ½	—	—	—	—	—	—	2	4.6	2.2
A	1 ½	3.5	4.0	4.6	4	5	7	1	4.0	1.2
	1	—	—	—	—	—	—			
	0.9	3.2	3.7	4.6	4	5	7	—1	3.6	0.9
	0.8	3.1	3.4	4.2	3	4	6	—2	3.1	0.8
	0.7	2.4	2.9	3.8	2	3	4	—3	2.7	0.7
	0.6	1.7	2.3	3.1	2	2	2	—4	2.1	0.6

respect again they resemble the *c* workers. Thus by comparison with the October ones, these show a more sustained period of initially high *g/d* ratio growth, and attain thereby a slightly higher average size.

The two slightly unusual workers had normal A periods, B periods of 2 and 3 days and C periods of 1 day. Their chief difference lay in their higher initial weights (3.0 mg) although the brain position of 0.6 was normal. They defecated to give adults only slightly heavier than average (5.0 mg) which meant that in their 8 and 9 days of growth they maintained a rather low specific growth rate. In essentials they behaved as the others.

(c) *The intercastes*.—Altogether 8 intercastes were produced: 6 in December and 2 in January. Considering first the average maturity series (Table 7): the A period does not differ substantially from normal, and the B period comes very near to it. In fact there were 3 cases of five days, 1 of four and a half days, and 4 of four days, but few of them were the typical queen type of series (viz. 1, 1 ½, 2, 2 ½, 3). The series of 4 days tended to be accelerated in the second half rather than in the first, so that the value 2 ½ or 3 often escaped record in the daily

examinations. Two of the 5 day series were atypical: 1, 1 1/2, 1 1/2, 2, 2 1/2, e, d and 1, 1 1/2, 1 1/2, 2, 2, e, d. But it is in the longer B period that the main differences from the worker occur.

The specific growth rate (Table 7, fig. 2) of these intercastes is on the average hardly less than that of February grown queens, but when combined with a short B period, it has the effect of causing a smaller average sized adult. It is noticeable (fig. 3) that these intercastes differ from the spring grown ones in diverging from the queen path much earlier: one may speculate to the effect that in spring any individual of such low potential

TABLE 7. — Weights and wing areas averaged per term of the standard maturity series for 8 intercastes produced from the mid-winter culture of large larvae; also weights and maturity indices averaged day by day using the start of the B period as origin.

PERIOD.	STANDARD maturity series.	WEIGHT.			WING AREA.			DAYS from origin.	DAILY mean weight.	DAILY mean maturity.
		Min.	Mean.	Max.	Min.	Mean.	Max.			
C	d	4.7	5.3	6.0						
	e	5.6	6.5	7.1						
	t	—	—	—						
B	3	6.0	6.8	7.2	9	15	21	5	6.2 (1)	2.8
	2 1/2	5.9	6.2	6.7	9	14	20	4	6.4	2.6
	2	5.5	5.6	6.2	9	13	18	3	5.6	1.9
	1 1/2	4.8	5.1	5.3	9	10	13	2	5.0	1.5
	1	4.0	4.5	4.9	6	7	9	1	4.5	1.0
A	0.9	3.2	3.9	4.4	4	5	7	—1	3.8	0.9
	0.8	2.7	3.5	4.4	3	4	6	—2	3.2	0.8
	0.7	2.3	3.0	3.8	2	3	4	—3	2.6	0.7
	0.6	2.0	2.2	2.6	2	2	3	—4	2.0	0.6

(1) This weight is less than the preceding as some individuals were in the e phase.

growth would have been deflected into the worker path before it reached this stage.

The average wing is below typical queen value before the start of the B period and abruptly reduces its rate of growth at the 2-segment leg stage again. As before, there is a general correlation between ovary size and wing size. Thus the intercaste (January) that had ovaries of 8 + 8 ovarioles behaved in this respect as did the spring individuals of comparable form, reaching a wing of 23 by the end of the B period and being normally queen-winged at the 2-segmented leg stage. The intercaste with ovaries of 3 + 7 ovarioles (again a January one) reached a wing of 22 and was also normal queen-type at the 2-segment leg stage so that the connection is not very precise. The intercaste with 5 + 5 ovarioles in its ovaries (December grown) on the other hand had a 14 wing at the 2-segment leg stage (normally the wing is 16 here) which was not observed to increase

although it is possible that it did and escaped detection (for it developed very quickly) failing to record a 3-segment leg stage. The intercaste with ovaries 1 + 2 reached a wing area of 12 units at the 3-segment leg stage, being well under size (10 units at the 2-segment stage). Finally, the four 1 + 1 ovariole intercastes that were really very like workers gave wings of 9, 12, 12 and 14 so that again the relation wing area/ovary size is not precise—only a correlation. As far as possible, these individuals have been illustrated (fig. 5) so as to show the variation that exists.

(d) *The queens.* — The queens from this set of cultures have acquired a developmental schedule very near that of the February cultured ones, even in the B period. Here 11 gave a full five-day period, 1 a four and a half day period and 4 a four day period. However, one of the five-day ones was anomalous: 1, 1, 1½, 1½, 2, e, d, there being little or no growth after the stage 1½ (5.8 mg) to 2 (6.1 mg). The final adult, although not perhaps a "microgyne", was, with 5.7 mg weight, very much below average. In the C period

the shorter one-day period prevailed (10 cases) and there were 6 of two days and 1 of one and a half days. The average weight after defecation (Table 8) was less than that of February-grown large queens, apparently on account of an inability to maintain their initial high specific growth rate, for the reduction of this in the B period was considerable though gradual (fig. 2). As they have nearly the same maturity schedule as the February grown ones, this shows up in the g/d relation too (fig. 3).

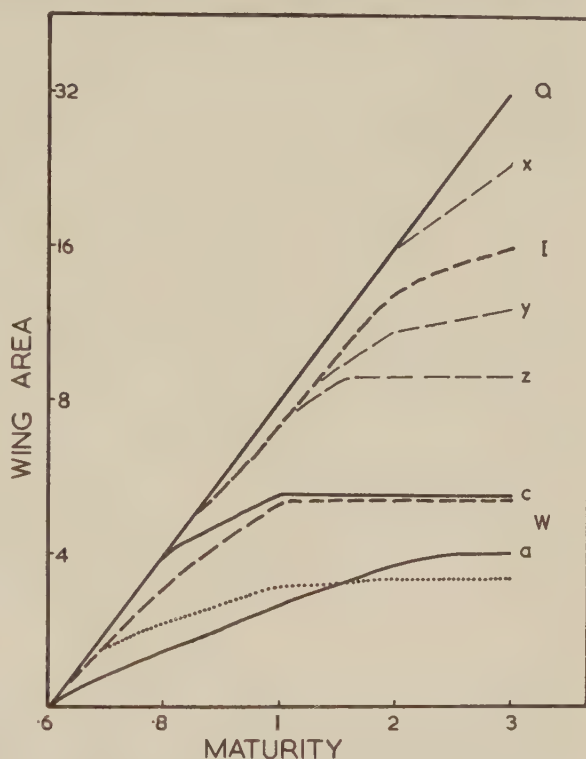


Fig. 5. — Wing growth in relation to maturity; of October large larvae (dotted) giving workers (W); of mid-winter large larvae (broken) giving intercastes (I) and workers (W); and of 3 selected February groups (full line): the Q set of queens (top), the c workers (middle) and the a workers (bottom). The queens from mid-winter larvae showed wing growth identical with those from February cultures. Three types of intercastes have been shown; with ovaries of average ovariole number: x, 5 to 8; y, 1½; and z, 1. Ordinate: wing area in arbitrary units on a log scale; abscissa: standard maturity series.

The wing growth appears normal in every way (fig. 5), confirming that the wing is the best single index in the larval stage of the coming adult form.

TABLE 8. — Weights and wing areas averaged per term of the standard maturity series, for 16 queens produced from the mid-winter culture of large larvae; also weights and maturity indices averaged day by day using the start of the B period as origin.

PERIOD.	STANDARD maturity series.	WEIGHT.			WING AREA.			DAYS from origin.	DAILY mean weight.	DAILY mean maturity.
		Min.	Mean.	Max.	Min.	Mean.	Max.			
C	d	5.7	6.9	8.1						
	e	5.1	7.6	9.6						
	t	6.6	7.3	7.9						
B	3	6.7	7.6	8.9	25	31	41	5	7.5	3.0
	2 ½	6.3	7.2	8.2	20	24	30	4	7.2	2.6
	2	5.6	6.6	8.2	13	17	21	3	6.6	2.0
	1 ½	5.3	6.0	7.5	11	13	18	2	5.9	1.5
	1	4.7	5.2	6.7	5	9	12	1	5.2	1.0
A	0.9	3.8	4.5	5.5	4	6	8	— 1	4.5	0.9
	0.8	3.1	3.8	4.5	3	4	6	— 2	3.7	0.8
	0.7	2.6	3.0	3.5	2	3	5	— 3	2.9	0.7
	0.6	1.7	2.2	2.8	2	2	3	— 4	2.2	0.6

GENERAL CONCLUSIONS.

Thus vernalisation confers a higher specific growth rate and a lower development rate on large female larvae. This happens progressively, affecting the earliest A stages first (contrast the October and the mid-winter workers), and then extends to the whole A stage and begins to affect the B period giving a larger animal with larger wings at the start (mid-winter intercastes). Lastly, the duration of the B period and the growth increment therein is increased (January queens, and ultimately the large February queens). The removal of diapause must occur during winter, but as it is virtually over in some of the largest individuals long before winter, its elimination cannot be considered the prime effect of vernalisation.

In general, the size of the wing at the start of the B period is closely correlated with the size of the larva, but a marked exception to this (one of the two anomalous workers), which although as heavy as a queen-forming larva at the end of the A period had only a wing of 4 units, suggests that wing size may be more closely related to growth rate. Similarly, worker number 24 of the *d* spring culture group had a large weight and low growth rate at the end of the A period although its wing never exceeded 4 units. The queens of the *q* group are converse cases of high specific

growth rate and large wings for their body size. Hence in general high specific growth rates, large wings for the body, and slow development rates are associated, and characteristic of queen-forming individuals. These may of course all result from a single influence such as the renewed activity of the *corpora allata*.

The c group of spring workers might be regarded as female larvae that even by February had not completed vernalisation. But there are objections to this view: they come from the group of medium larvae, they have rather a low development rate in the A period, and the sudden deflection from the queen path at the end of this period is not accompanied by any reduction of specific growth rate, merely a sharply accelerated development. It seems best to regard them as individuals that are the victims of the intercaste avoidance process (BRIAN, 1955 a) rather than partially vernalised types.

The question of the development of this "switch" mechanism that in February and later months acts to divide the ontogenies into worker- and queen-forming streams may be considered further. In the February and later cultures only 6 intercastes were produced out of 55 females incubated, and even this was considered an unnaturally high value (BRIAN, 1955 a). In the December set of 14 ontogenies, 6 were intercaste yielding, a proportion significantly higher (by χ^2 test P: 0.01-0.02). It must be presumed that the switch mechanism is itself created during vernalisation. Perhaps it is in the nature of a period of trial during which the capacity of the individual for queen-formation is assessed, and after which it is allowed to proceed as before if successful, but deflected towards the worker-form by acceleration of development or growth inhibition if unsuccessful.

Of course, all larvae are not at any one time in the same stage of vernalisation, for partly-vernalised ones (giving intercastes) can be obtained either in December or January. Nevertheless, it appears that the major change occurs in the relatively short period about the end of December. That is not to say that further improvements are not made later, such as those that increase the queen size.

Dehydration during autumn has tended to obscure the clarity of these results, and the first two days (but not more) may show spurious weight gains due to rehydration. The higher specific growth rate after winter is, apart from this possible source of error, undoubtedly genuine. The action of winter on workers and larvae together releases them from their various inhibiting influences, and in spring it is temperature alone that prevents a resuscitation of activity.

QUEENS FROM EGGS

The validity of these facts is confirmed by the production of queens from eggs laid in the laboratory.

An egg production unit was set up consisting of a queen of *Myrmica rubra macrogyna* and 20 workers taken from a mature nest. Eggs were removed periodically in batches of 100 to 150 and given to groups of 100 vernal workers from the same nest. Such egg/worker ratios have been shown (BRIAN, 1953) to confer maximal advantage on the larvae. Brood corresponding in every way to the large larvae of winter colonies was produced, and, with the workers, was vernalised at 4° C for three months. Then the workers were given 3 weeks preparation in culture conditions before the larvae were added. In all of 5 serial replicates only workers and males resulted. The defect lay in the worker population.

This experiment was repeated with a colony that had been allowed to rear its winter larvae, and whose worker population consisted as a result of (at least) two age groups. The final outcome was that the majority of larvae produced queens, only a few males and workers following these.

Although this has not been the subject of critical analysis, it seems probable that the young workers played an essential role, and it is likely, although not certain, that this was in the nurture of the vernalised larvae in the final stage of culture rather than in the pre-diapause phase for the large larvae were indistinguishable from their natural counterparts and from those of the earlier set of cultures. The older age group of workers, after what must have been their second winter, were no doubt incapable of giving appropriate attention to the larvae; in fact they were probably senescent (BRIAN, 1951).

Thus it is possible in the laboratory, provided attention is paid to a number of conditions, to produce queens. It is manifest, however, that this depends on steering them throughout their ontogeny through a quite circumscribed set of environmental influences, many of which remain to be investigated, such as the effect of queen age and of season on egg potentiality (vide GOSSWALD and BIER, 1954), on the possibility of a more specific action by the young workers and on many other factors both of a qualitative and quantitative nature. These laboratory-reared queens have resulted from employing the most probable and generous culture conditions; it remains to discover how much these can be reduced, so that a more precise formulation of the limits of environmental licence can be obtained.

DISCUSSION

In *Myrmica rubra* L. it is vernalisation of the third instar larva that is an essential prerequisite of queen formation. In *Formica rufa rufopratensis minor* Gössw. it is the queen-mother that must undergo this process in order that queen-potential eggs rich in food reserves may be produced (GOSSWALD and BIER, 1954). Queen-potential that is to say in the society in which they would normally develop: for transference of

summer eggs of the above species to vernal workers of *F. rufa pratensis* RETZ. results in the production of queens and intercastes.

Whether or not this vernalisation of the queen takes place in *Myrmica* is unknown, but such evidence as there is suggests that this is not the case. Thus as has been shown, small larvae transferred in September to vernal workers of the same species (at 20° C) change them into large winter larvae resembling those that produce queens.

On the other hand, vernalisation certainly is not necessary for tropical species and one is led to speculate on its utility to temperate forms. In the case of *M. rubra* it can be reasonably supposed that it prevents any large larvae that escape the suppression of diapause becoming queens at an unsuitably late time of year: they produce useful workers instead. In *Formica rufa* too, the same explanation appears probable: that it gears the brood cycle ensuring that queens are produced, matured and disseminated as expeditiously and successfully as possible. Thus whereas vernalisation appears likely to be common to all temperate ants, diapause is specifically associated with the partial 2-year life-cycle characteristic of *Myrmica*, *Leptothorax* and others.

In various species of *Polistes* one of the principal distinctions between females is whether they enter diapause or not (DELEURANCE, 1950, 1952). The first to be produced start work on becoming adult, the later remain relatively inactive, hibernate and initiate colonies in the following spring. Thus the change from rapid to retarded individuals, from worker-formation to queen-formation resembles the first part of the seasonal cycle of brood of *Myrmica* (although affecting larvae in the third instar in this case). But it does not affect the ultimate caste as it does in *Myrmica*, for this is determined in the larval stage: that is diapause and vernalisation follow caste determination rather than precede it. The last, DELEURANCE suggests, is influenced by temperature and worker type which act through the quality of the food given to the larvae. The role of temperature may of course be much greater in nearly homiothermic wasp nests than in poikilothermic ant colonies, a gradual rise in temperature taking place in summer due to population increase as well as to the changing position of the earth in relation to the sun. Similar situations exist in all probability in all temperate and annual colonies of the social Vespidae and Bombidae, as well as in the well known case of *Halictus*.

It is no doubt that diapause (which affects so many stages in social insects) and vernalisation are placed in life-cycles in such a way as to confer maximum overall efficiency and that the resemblances that have been discussed are purely superficial. And yet, the rather common association in social Hymenoptera of diapause with full sexuality in the females (*Apis mellifera* is of course an exception to this) and the increasing evidence that trophic factors are at the root of polymorphism certainly points to the possibility of caste and diapause being a common consequence of a specific nutritional régime.

An instance of this in the non-social Hymenoptera is found in the internal

parasite called *Melittobia chalybii* where the females are either brachypterous and non-diapausing in the larval stage or alate and diapausing (SCHMIEDER, 1933). The first larvae, feeding on the blood of the host, develop rapidly into the brachypterous form; the later ones (many from the same parent), feeding on the solid tissues, develop into alate forms after a diapause of about two months in the larval stage. SCHMIEDER has shown that these alternatives are completely dependant on the quality of the larval food.

Comparison with *Myrmica* suggests that the rapid brood first produced by the ant might be fed on a more liquid and assimilable food perhaps containing more sugar and more worker-laid eggs or pharyngeal secretion whilst the later brood receives a diet with less water, less sugar, and more crude protein (flesh). The importance of worker-laid eggs has already been discussed (BRIAN, 1953). SIMMONDS (1946) has shown that a sugar rich diet causes females of *Cryptus inornatus* (Ichneumonidae) to produce eggs, fewer of which, at a later stage (in the cocoon), enter diapause than if the female parent was supplied with a source of protein. Other cases only slightly less relevant here have been reviewed by ANDREWARTHA (1952). Thus whilst it has been possible in this paper to show that worker type and temperature affect diapause, further analysis of their nutritional action is desirable.

The period of low temperature treatment at 0-15° C that is favourable to diapause development (ANDREWARTHA, 1952) in many insects has been shown to have a similar action in *Myrmica*. But in the ant it does more than remove diapause as has been shown; it is an essential step in queen-formation and for this reason it has been necessary to distinguish vernalisation from diapause.

These results suggest that diapause as completed in October is sufficient to reactivate (via the brain, no doubt) the cell division and differentiation hormone (from the prothoracic glands or their analogues) but not the hormones favouring larval growth (or perhaps it is better to say larval expansion to distinguish this growth from that due to mitosis) which it has been suggested (BRIAN, 1955 a) might be the juvenile hormone from the *corpora allata*. Vernalisation would then be the process that restored the latter's activity.

Summary.

The factors influencing the size of hibernating larvae have been investigated. The large ones are formed early in summer, become quiescent at an important developmental stage known as brain position 0.5, and then pass through a period of slow growth characterised by high ratios of growth rate to development rate. They can be forced to metamorphose by vernal workers or temperatures as high as 25° C when they always yield workers. The medium larvae are formed after the large, and have reached the quiescent diapause stage (brain 0.5) before winter.

The small larvae are formed last of all, and do not reach this stage before winter. They are plastic, and their development can be influenced experimentally by varying the worker type and the incubation temperature. Male larvae do not have a diapause.

Vernalisation is an essential step in the queen formation process. The ability of large female larvae to sustain a high ratio of growth rate to development rate increases gradually from nil to full during winter. Males and the smallest female larvae are, on the other hand, unaffected. Vernalisation also develops the mechanism by which intercastes are avoided.

Résumé.

On a déterminé les facteurs qui influencent la taille des larves d'hiver. Les grosses larves qui apparaissent au début de l'été deviennent quiescentes à un stade ontogénétique important désigné par : ganglions cérébroïdes 0.5 ; puis elles passent par une période de lent accroissement que caractérise la haute raison de la vitesse de l'accroissement par rapport à celle du développement. La métamorphose peut être produite par l'action des ouvrières vernaies ou par des températures assez hautes (25° C) ; de telles larves donnent surtout des ouvrières. Les larves de taille moyenne se produisent après les grosses larves, et elles atteignent le stade de la diapause (ganglion cérébroïde, 0,5) avant l'hiver. Les petites larves se forment les dernières et n'atteignent pas ce stade avant l'hiver. Elles sont plastiques et leur développement peut être modifié expérimentalement si l'on change le type d'ouvrières nourricières et la température d'élevage. Les larves mâles ne subissent pas de diapause.

La vernalisation est un processus essentiel pour la production des femelles (reines). La faculté des grosses larves femelles à soutenir une haute raison de la vitesse de l'accroissement par rapport à celle du développement augmente peu à peu, pendant l'hiver, de zéro jusqu'au maximum. D'autre part, les larves mâles et les plus petites larves femelles ne changent pas. La vernalisation développe aussi le processus par lequel sont évitées les intercastes.

Sumario.

Por examinación de los factores que influyen el tamaño de las larvas en invernación, se ha determinado que las mayores se forman en la primera parte del verano y quedan durmientes durante un importante estado del desarrollo conocido como (posición cerebral 0,5). Luego pasan por un período de crecimiento lento caracterizado por alta proporción de crecimiento a la proporción de desarrollo.

Puédese enforzar su metamorfosis, por medio de trabajadores vernaies o temperatura hasta 25° C cuando rinden siempre trabajadores.

La larva mediana fórmasse después de la mayor y llega al estado durmiente del (diapause) cérebro 0,5 antes del invierno.

La larva menor es última en formarse y no llega a este estado antes de comenzar el invierno. Debido a su plasticidad, se puede influir su desarrollo experimentando con la variación de los trabajadores y la temperatura de incubación. Larva del sexo masculino no pasa por este estado.

Vernalización es un paso esencial en el proceso de formación de la reina. La habilidad de la larva hembra mayor de sostener un alto porcentaje de crecimiento hasta llegar al de desarrollo, se aumenta gradualmente de cero para completarse durante el invierno.

Mientrastanto, los machos y la larva hembra menor quedan sin afectarse. Asimismo la vernalización asiste al desarrollo del mecanismo por el cual se evita fecundación cruzada.

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THE PATTERN OF COLONY FOUNDATION IN THE ARCHAIC ANT *MYRMECIA REGULARIS*

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INTRODUCTION

The method of colony foundation among ants of the primitive subfamilies Myrmeciinae and Ponerinae is of great interest to the student of the phylogeny and social organization of the Formicidae, for two quite different reasons. First, these subfamilies include the most primitive and generalized among ants. In the absence of those solitary and semisocial forms which are of such importance in revealing the stages by which colonial life arose among the wasps and bees, the temporarily solitary colony-founding myrmeciine and ponerine female undoubtedly offers the best evidence available of the manner of inception of social life in the Formicidae. This point has often been emphasized and the subject has received correspondingly careful study. Observations on colony foundation were made under natural conditions by Wheeler early in this century in the genera *Odontomachus*, *Anochetus*, and *Neoponera*. In 1914 and again in 1931, Wheeler made field observations on colony foundation in two of the most archaic of all genera of ants, *Myrmecia* and *Amblyopone*, and drew significant deductions from them (1916, 1932, 1933). He also investigated the colony-founding behavior of *Brachyponera lutea*, of the Ponerini—a form remarkable among Ponerines for the striking difference of stature between the females and workers. Tepper (1882), Froggatt (1915) and Clark (1925-7, 1934 a, 1951) have all described the nuptial flight in the larger species of *Myrmecia*, and Clark has reported various field observations with respect to colony foundation. Haskins (1941) and Haskins and Haskins (1950 a, b, 1951) have observed the cycle in some detail in the artificial nest in *Bothroponera soror*, *Brachyponera lutea*, *Amblyopone australis* and *Myrmecia forficata*. The conjectures of Wheeler in his hypothesis concerning the "normal" method of colony foundation in *Myrmecia*, *Odontomachus*, and among other Ponerinae—and therefore presumably the primitive one among ants—have been thoroughly substantiated in this wide range of forms. Typically, the winged female flies from the nest in swarms or irregularly and individually, is fertilized and thereafter constructs a cell in earth or wood. In sharp

contrast to the "claustral" mode of colony foundation common among higher ants, this cell is not permanently closed, and the female frequently forages from it. Eggs are laid, tended and hatched, and the young fed to a considerable extent on prey freshly captured and brought in by the parent. Replacement of the flight muscles of the female with fat body occurs much as in the higher ants, as Haskins and Enzmann (1938) have shown. It has been found that at least in the genera *Euponera* (Haskins, 1931), *Odontomachus* (Haskins and Haskins, unpublished), *Ponera* (Le Masne, 1952) and *Myrmecia* (Haskins and Whelden, 1954) adults are capable of regurgitating ingluvial food to the young, and in *Odontomachus* such nourishment, derived from the tissues of the queen, is of significance in the rearing of the first brood. It is now clear that this is also true of *Myrmecia regularis*. The condition of claustral colony initiation, so typical of the higher Formicidae, has been derived by a process of relative specialization of certain elements of the colony-founding pattern already present in the most archaic of living ants.

The second point of particular interest in the pattern of colony foundation in the Myrmeciinae and the Ponerinae is of a more special character. These subfamilies are peculiar in the number of species showing retention in evolution and specialization to an auxiliary or even the sole reproductive role of forms intermediate between the primitive winged female and the typical worker. In such specialized types as certain members of the genus *Leptogenys*, the alate female is rare or may have entirely disappeared, its function being assumed by one or more stabilized ergatogynes with hypertrophied ovaries and fat body in each colony. In the interesting genus *Rhytidoponera* it is possible, as Brown (1952) has pointed out, to assemble series of species at one end of which normal winged females occupy the usual reproductive role, while at the other such females are exceedingly rare or altogether wanting and the reproductive function is shared among certain worker-like members of the colony, which show no obvious external morphological differentiation from their fellows, but are specialized internally to the retention of sperm and mate regularly.

The frequency with which ergatogynes occupy an extremely important position in the reproductive economy of primitive and archaic ants, in many cases partly or entirely replacing the winged female, contrasts rather strikingly with their comparative rarity among higher forms, except those which are permanent social parasites. It seems possible that one contributory factor in this unusual evolution has been the non-claustral pattern of colony inception which was apparently characteristic of the earliest ants and is still widely retained among archaic types, even when the fully winged female is no longer the dominant reproductive form. It seems probable from the evidence quoted earlier that the transformation of wing tissue to fat body to serve in sustaining the queen and in nourishing the first brood occurred in Formicid evolution before the perfection of the claustral mode of colony foundation. Thus this source served only as an auxiliary metabolic reserve. Main reliance was evidently placed, as it

still is in *Myrmecia* and many ponerines, on external sources of food continuously exploited during nest-founding. Under these conditions, reduction or loss of the wings in the fertile female, with corresponding alterations of the thorax, particularly those involving loss of flight muscles, would be compatible with persistence of the ancient method of colony establishment. In such an evolution, the advantage of wide flight dispersal for the species might well be compensated by hypertrophy in the young female of a habit of wandering extensively on foot, and the disadvantage in the loss of food-reserves represented by bulky wing muscles might be more than compensated by the reduction of hazard to the queen in the early critical period. Hence such a development may well be adaptive at this stage of evolution. Once the habit of claustral colony foundation has become fixed, however, large and bulky wing muscles are a *sine qua non* of survival for the young queen. While ergatogynes may still serve a supplementary reproductive function in established communities, the establishment of new colonies by isolated ergatogynes becomes improbable. It seems not unlikely, therefore, that wings and their bulky flight muscles have been of evolutionary significance in the Formicidae not only as organs assisting in dispersion and wide cross-fertilization but also, and perhaps more importantly, as food reservoirs permitting the development of the pattern of claustral colony-foundation and, by the same token, restricting that pattern to alate females, and thus, perhaps, tending to maintain and to sharpen the female dichotomy so characteristic of higher ants.

The genus *Myrmecia* illustrates this linkage between non-claustral colony foundation and the "permissive" reduction or loss of alation in the fertile female unusually vividly. Colony foundation has been investigated in detail in only a few species, but there is good reason to suppose that the non-claustral habit is widespread. Concomitantly, there is perhaps no single genus of ants in which such a rich series of examples of loss of wings in the fertile female can be assembled, as Clark (1951) has recently re-emphasized. Subapterous and brachypterous females occur in many species, often coexisting with fully winged forms and in frequencies ranging from extreme rarity to complete replacement of the alates. Essentially all stages of reduction of wing musculature and thorax can be found, culminating in full ergatogynes, superficially closely resembling the workers, but evidently fertile, like the corresponding ergatogynes of *Rhytidoponera*. In such a species as *Myrmecia aberrans* no alate or brachypterous female has ever been found, according to Clark, and it seems likely that the ergatogyne is the sole remaining female reproductive of the species.

Details of colony foundation, as observed in the artificial nest, have been presented for a species of *Myrmecia* (*M. forficata* Fabr.), in which the fully alate female undergoes a rather specialized nuptial flight (described by Clark, 1951, p. 19) (Haskins and Haskins, 1950) (1). It seemed of

(1) Clark (1951) has emphasized that the alate is not the only form of fertilized female in *M. forficata*. The alate was the only form observed, however, in the populations used in that study, which were taken from the vicinity of Melbourne, and from the lower slopes of Mt. Kosciusko.

particular interest, therefore, to investigate colony-founding behavior in a species in which wing-reduction in the female is well advanced. *Myrmecia regularis* Crawley offers an excellent example of this condition. Its females show much reduced thoracic development, and are described by Clark (1951) as subapterous, indicating that wings are present in the adult only as relatively undifferentiated buds or are wholly wanting. Actually, as described below, the females in the populations from Manjimup on which this study was made bore well-developed wings, though much smaller than normal. They were also highly deciduous.

Myrmecia regularis is in some sense classical material for a study of this kind, for it is the species on which Wheeler largely based his brilliant generalizations concerning colony-founding among primitive ants in general (1). The account of colony foundation presented here is based on observations in the field and in the artificial nest extending over six years.

The Young Queen. Exodus from Parent Nest.

Myrmecia regularis is one of the larger members of the genus. It was originally described by Crawley from specimens taken at Albany, and throughout the moist forests of karri and jarrah it is a common—and indeed a dominant—form. Head, thorax and pedicel are red, the gaster black but in life with a bronze tinge with a cast of iridescent violet, more evident during the summer, and the final segments showing broad golden-yellow bands at the posterior margins on the dorsal surface. The thorax of the female is reduced, though the typical elements are still obvious, concomitant with a considerable reduction in the wing musculature. The wings are short—they may be vestigial in some populations (Clark 1951), but this was not true of those examined at Manjimup.

Clark (1925-7), Wheeler (1933), Barbour and Loveridge (1929) and Haskins and Haskins (1950) have all described the mature colonies of these earth-nesting ants, which characteristically are built in damp black soil under large logs, from which the aggressive workers sally out in numbers at the least disturbance. So far as we are aware, however, no accounts have been published of the "nuptial flight" of the species, probably because the observations were not made at the time when the winged forms appear in the nests. At Manjimup, West Australia, this takes place during March.

During the middle of March 1948, numerous mature colonies of *M. regularis* were examined in the forests about Manjimup, in the same locality from which Barbour and Loveridge (1929) described the occurrence in these communities of the small and exceedingly interesting wholly terres-

(1) Ironically, the skillful deductions of Wheeler fit almost perfectly the primitive colony-founding pattern of a species with alate females, such as *M. forficata*, but are not strictly accurate for the species which furnished a large share of the evidence for them.

trial Anuran, *Metacrinia nichollsi* Harrison—an occurrence fully confirmed in the course of these examinations. In many of these large nests numerous males were present in the upper galleries, evidently waiting to take flight. They did so actively when the nests were disturbed. Together with these males, considerable numbers of rather callow, yet wingless females were crowded into the superficial chambers. They showed clear evidence of dealation (which must have occurred very early in life) in the well-defined stumps of both primaries and secondaries. Despite their winglessness, they gave every evidence both of extreme youth and of being poised ready to leave the parent nests.

On March 14 a colony was examined which contained over twenty of these females. Among them was a single exceedingly callow specimen which still bore the small and rather weak but well developed wings. Near this colony a fully pigmented isolated female was taken in a cell under conditions precisely like those described by Wheeler and a bit further away an incipient colony was found, consisting of a young queen and six rather small workers.

Six of the dealate, callow females were removed from several colonies and isolated in artificial nests under conditions which offered abundant opportunities for the founding of colonies. When they showed little disposition to excavate, earthen cells were artificially constructed for them. All exhibited at first a pronounced tendency to wander extensively in the open from early evening until late at night. Gradually, however, these periods of wandering contracted, and eventually the females left their cells only to feed. No eggs were laid, however, and after six months all had perished. Histological examination disclosed that the wing musculature was still largely intact. Control examination of the wing musculature in virgin females of *Myrmecia vindex* as compared with females in established colonies has shown that in this species the wing musculature entirely disappears in mature fertilized females, being replaced by fat cells oriented to fill the resulting cavities. It was also determined histologically that the spermatheca of one of these young females was empty of sperm, in contrast to the normally well-filled spermatheca of a young fertilized colony-founding female.

It seems very probable that these numerous dealate females in populous nests were in fact young, virgin individuals which had shed their wings within the parent colony preparatory to emerging and wandering. It seems probable (but has not been actually observed) that during this wandering period fertilization by the active low-flying males takes place on the ground, apparently the typical pattern for the brachypterous female of *Myrmecia tarsata*. Only after this period of preliminary wandering does the now fertilized female isolate herself and proceed to the establishment of a colony in the fashion typical of the genus. This these infertile young queens, prematurely confined, proved unable to do. These presumptions were strengthened by field observations made in the same locality, and in the artificial nest, several years later.

The "Fine Structure" of Colony Foundation.

On May 25, 1952, an extensive search was made for *Myrmecia regularis* in the same area of woodland about Manjimup. This was the beginning of the ill-defined winter dormant period. Foraging occurred, and there was no sign of actual hibernation, but the aggressiveness so characteristic of larger colonies was considerably mitigated and it was possible to examine them much more closely. In the few mature colonies which were fully excavated, only one fertile female was found, casting doubt on the assumption of Haskins and Haskins (1950) that the species is normally pleometrotic, and in strong contrast to the numbers of dealate females found in larger nests in the late summer of 1948. Also in striking contrast was the fact that isolated colony-founding females, of which only one could be found in 1948, were now relatively abundant in their typical double chambers under logs or stones. These corresponded exactly in form, location, and habitus with those described by Wheeler from the forests about Margaret River and Pemberton in November 1931 (1933). Like these, the chambers of the Manjimup females occasionally contained a few eggs or larvae, but were more usually empty of brood. Ten such females were taken, together with their brood where present, and brought to New York, where in mid-June they were isolated in earth-containing Lubbock nests, $6'' \times 8'' \times 3\frac{1}{4}''$, each placed in a glass-covered shallow drawer $8'' \times 12'' \times 1\frac{3}{4}''$, which served as a foraging arena. A supply of dilute honey was kept constantly available, and fresh insect food was furnished three times a week.

Unlike the females taken in 1948, none of these ten individuals exhibited any generalized tendency to wander outside their nests. All promptly excavated chambers of as nearly the typical form as the constricting geometry would allow. Some closed these cells during the day, others left a narrow permanent opening. All emerged early each evening to feed on honey, but returned promptly as soon as full fed. Half the nests were kept at room temperature from the beginning (18° to 23°), while the other half were kept in an incubator at 12° C until early September (September 7 and 11) when they were brought to 18° C. The latter group, though initially retarded, later proved the more completely successful in colony foundation.

All females, including those held at the lower temperatures, produced eggs within a month of isolation. These were arranged individually on the floor of the chamber in the typical manner of the genus and carefully tended until hatched. Foraging for insect food began within a day or two of the hatching of the larvae and continued until the entire brood was enclosed in cocoons. During their entire period of growth larvae were fed by regurgitation in addition to the insect food. This point was shown very clearly by incorporating small concentrations of methylene blue in the honey source, as described elsewhere. (Haskins and Whelden, 1954.) The larvae of

females supplied with this dye showed a deep blue staining of the contents of the hind gut throughout growth.

The hatching callow workers were given some assistance in eclosion by the parent. The degree of callowness varied widely, some individuals becoming almost fully pigmented within the cocoon while others were noticeably pale and weak for several days after emergence. Empty cocoons, like waste food material, were scrupulously removed from the nest by the parent, usually within an hour of hatching. Very young callows were occasionally carried about by the female (as also by older workers) but within a few hours this attention had ceased. Callow workers were seen to forage outside the nest within a few hours of hatching, and continued to do so regularly. The parent females were several times observed to feed independently outside the nest, or to aid in foraging, for several days after their first-brood adults were also foraging actively. There is thus a considerable overlap between the assumption of foraging duties by the workers and their relinquishment by the female. In the event of premature loss of the first brood, the foraging pattern may persist until a second group of young adults appears. Gradually, however, the female ceases to forage. In mature colonies there is good evidence that the queen never leaves, receiving nectar by regurgitation from the workers, and protein and fat probably both ingluvially and directly from the prey brought in and perhaps, from the exudates of the larvae, which are freely licked.

Of the nine females permitted to found their colonies in normal fashion, all reared larvae to the stage of spinning cocoons, and seven produced young workers. Three of these, which had been held at room temperature from the beginning, matured the first workers on November 13, 1952, and March 1 and March 28, 1953, approximately five and eight months, respectively, from the initiation of colony foundation. The remaining four, which had been kept at 12° C until September, eclosed their workers respectively on January 8, January 18, January 26, and January 30, 1953, six and seven months after colony initiation. Three of the females produced two workers in the first brood, one three, two four, and one five (1).

It is believed that the normal period required for colony foundation is five to six months, though wide variation is probable. The normal first brood is probably at the upper end of the series, or somewhat larger, though this too may show wide variation. It was not possible to control the humidity accurately in these experiments, and the high humidity of a New-York summer caused heavy mortality among larvae transforming to pupae and during pupal life. This was clearly the most serious cause of the two failures in the series, and even among successful females a number of

(1) Is of interest that none of these first-brood workers was of abnormally small size, as is so characteristic of higher ants. All of them, indeed, were considerably larger than the smaller workers normally produced in mature colonies, and a few approximated the larger individuals in such well established communities.

cocoons were lost, reducing the size of initial broods brought to maturity and in several cases delaying their appearance. A typical time scale of colony foundation for these females is given below.

TABLE I.

Oct. 23 (1952)	2 eggs
Nov. 15	3 eggs
Nov. 21	9 eggs
Nov. 29	10 eggs
Dec. 8	3 larvae hatched
Jan. 8 (1953)	7 half grown larvae
Jan. 26	8 larvae nearly full grown
Feb. 3	First cocoon spinning
Feb. 6	Second and third cocoons spun
Feb. 14	4 cocoons; 3 larvae; 1 larva spinning
Feb. 23	6 (or 7) cocoons; 1 larva spinning
Mar. 28	2 workers hatched. (1 very callow) 14 eggs
Mar. 31	1 worker dead
April 6	Third worker hatched
April 13	Fourth worker hatched
April 16	Fifth worker hatched

The tenth female of this series was not permitted to found a colony normally, and yielded most interesting results. Its treatment was identical up to the point at which the first egg was hatched, on October 3. At this time, all external sources of protein and fat were cut off, to test how far the queen could (or would) carry the first brood on metabolites stored or elaborated from her own tissues. Dilute honey continued to be liberally provided. The performance of the queen, when thus forced to adopt the essentially claustral mode of colony foundation common in higher ants, was interesting. By October 12, six small larvae were present, fed ingluvially by the female and in good condition. They persisted, growing considerably, until October 23. On October 31 they were still surviving but were noticeably attenuated, while the parent, abandoning the usual crepuscular habit, foraged persistently and continually outside the nest during the daylight (as well as the night) hours. Finally, on November 15, forty-three days after the withholding of metabolites began, the female was found dead outside the nest. Within were five larvae, quite healthy but not well grown, which survived for a week longer. It was noteworthy that the parent female had depleted its own protein and fat store to a fatally low level on behalf of the larvae, and had at no time destroyed and eaten any portion of the brood to permit the rearing of the rest and its own survival. The latter contrast is particularly striking, since this is one of the most characteristic patterns of the queens of higher ants. In similar contrast, the eggs of the colony-founding *Myrmecia* queen are rarely if ever devoured. It is of some interest that an essentially identical pattern was followed by a colony-founding female of *Myrmecia mandibularis* also taken at Manjimup on the same day as those of *M. regularis*, except that in the latter case insect food was provided before the female perished.

Several conclusions are possible concerning the pattern of colony foundation in *Myrmecia regularis*. Some of them apply only to this species, representing specializations from a more general pattern. Others are typical for other—and possibly for all—members of the genus.

1. Young females of *M. regularis*, in contrast to the behavior pattern described for *M. pyriformis* (?) by Tepper (1882), for *M. gulosa* by Froggatt, reported by Wheeler (1916) and by Clark (1925-26, 1951) for several species with fully alate females, shed their wings within the parent nest while they are still callow, and remain in the superficial galleries at least for several days until they are hardened and pigmented. This behavior is correlated with shortened wings and reduced thoracic structure.

2. Thereafter the wingless young females leave the parent nests and pass a period of wandering in the open, during which they are fertilized by the active low-flying males, which differ little in structure and behavior from the males of various other species of the genus.

3. Once fertilized, young females excavate earthen cavities, usually under stones or logs, and close themselves in. These cavities are regularly reopened to permit the queen to forage. Under laboratory conditions, such young queens have been found to be crepuscular or nocturnal in habit, and to forage for nectar nearly every evening, both before and after eggs have appeared in the nest.

4. As is typical of other members of the genus, the eggs are subspherical and do not adhere in packets. They are arranged singly on the floor of the chamber and tended and handled individually. Though some eggs may be lost in the course of incubation, they are rarely if ever eaten by the female. The period of egg laying is rather sharply circumscribed, so that all eggs of a given group are nearly of the same age.

5. Foraging for insect food begins within a day or two of the time of larval hatching and continues until all the larvae are enclosed in cocoons, when it ceases rather suddenly. Very young larvae are fed extensively, and perhaps exclusively, with ingluvial food by regurgitation, as in higher ants, and it is very probably protein and fat depletion in the adult, after a day or two of such feeding, which initiates the behavior of hunting for insect prey. Ingluvial feeding of the larvae continues throughout their growth period, and it is probable that during this entire period the female (and the workers of older colonies) suffers constantly from depletion of metabolites—a condition which maintains the hunting behavior pattern throughout larval growth. It has been shown that, in the absence of available external proteins and fats, the food reserves of the female may be fatally expended on behalf of the larvae. During this period of serious depletion the hunting behavior of the female is much intensified. It may be added that hunting females regularly partake of the insect prey which they bring to the nest, sharing it with the larvae. By the same token, it is probable that a re-accumulation of fat and protein reserve occurs after the larvae have spun cocoons and their food demands have ceased, resulting in a rather abrupt drop in the intensity of the hunting pattern.

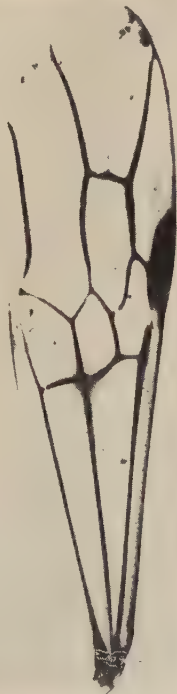
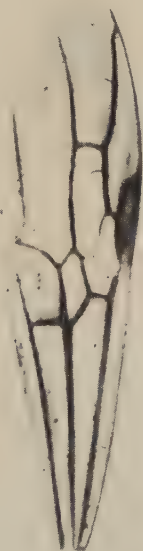
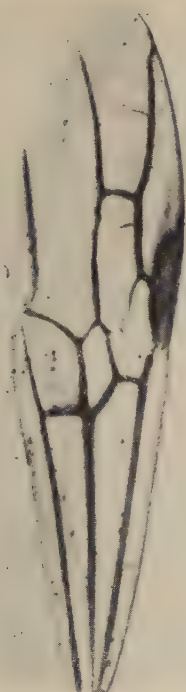
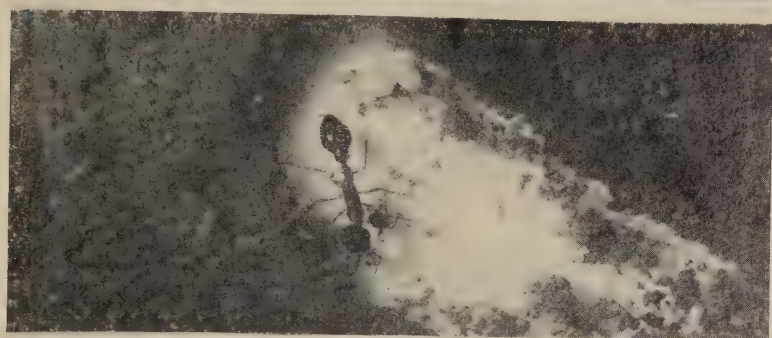
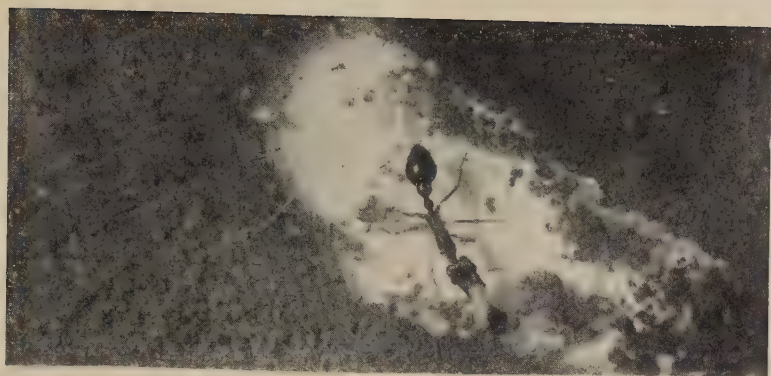
6. The enclosure of the first brood of larvae in cocoons commonly coincides with the beginning of physogastry of the queen and the laying of another group of eggs which will produce the second "generation" of workers. This behavior is consistent with the assumption that fat and protein reserves are "reaccumulated" by the female only when the demands of the larvae have ceased.

7. It is of interest that no matter how serious the food depletion of the queen, the larvae are not destroyed and eaten, and in cases of extreme deprivation they may survive the mother by several days. This situation is quite contrary to that in higher ants.

CONCLUSIONS

An examination of the "fine structure" of the colony founding behavior in *Myrmecia regularis* shows a number of features which are probably common to many if not all species of the genus, several of which have already been described. Such are the isolation of the young female in a closed cell which is opened at frequent intervals to permit foraging, and the rearing of the first larvae on a diet of insects and other Arthropods captured by the female. It has not been generally appreciated, however, that the larvae may be fed at first principally on ingluvial food and that ingluvial feeding continues to supplement the entomophagous larval diet throughout their lives. The fact that females, when deprived of external sources of protein and fat, can still rear broods of larvae part way to maturity shows that considerable quantities of metabolites are delivered to the larvae in this fashion. They must perforce be derived from the female nutritional reserve, and the depletion which results is evidently a major factor in determining the onset and the intensity of the adult hunting pattern.

Thus it is possible to find in the behavior-pattern of the colony-founding *Myrmecia* female every element of the typical claustral pattern of higher ants. The isolation of the young female and the early feeding of the first-brood larvae on ingluvial food differ in no essential way from the behavior of, say, *Formica subsericea*. The total pattern of claustral colony foundation could have been derived in evolution from that of *Myrmecia* simply through an increase in the nutritional reserves of the female relative to the survival and brood-rearing task to be accomplished, achieved by increase in the proportion of protein and fat reserves carried by the young queen and by the increased divergence of stature between the mother and first-brood young. With this added efficiency, ingluvial feeding of the young as their sole source of nourishment, possible in *Myrmecia* for only the first few days, can be extended without supplement throughout the whole growing period of the first brood. Efficiency in metabolite conservation, moreover, has been improved by the behavior of the queens of higher ants of regularly eating some of their eggs and young first-brood



larvae, permitting the rest to reach maturity. Perhaps the greatest evolutionary gain from these developments has been to make it unnecessary for the queen to forage—or indeed to expose herself above ground—once nest-founding has begun. The conservation in energy—and hence in energy sources—for the incipient colony is great. But even more important is the lessened hazard to the life of the queen, upon which the existence of the colony depends at this stage. The adaptive value of these developments is obvious. It is not nearly so surprising that they have occurred so widely among higher ants as that there should be surviving forms in the world like *Myrmecia* in which the generalized and hazardous pattern of fully exposed hunting has been retained—a condition no doubt associated with the formidable stings and agility of all the members of the genus, the crepuscular and nocturnal habits of many of them, and the striking coloration of others.

Myrmecia regularis departs in its colony-founding behavior from the primitive pattern of the genus in that the young females shed their wings within the parent nest, and later emerge to be fertilized and isolate themselves. This omission of a conspicuous nuptial flight very probably reduces the hazard to the young females without sacrificing the factor of dispersion, since they wander widely. The habit is associated with reduction of the wings and wing musculature, and the beginning of an approach to ergatogyne form. The retention of foraging habits in the female *Myrmecia* probably permits a flexibility of evolution in the direction of thoracic reduction which would not be possible in those higher ants where the habit of independent claustral colony foundation requires the retention of bulky wing muscles as an indispensable metabolite reserve during long months of forced deprivation.

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L'ENREGISTREMENT THERMIQUE CONTINU DANS LES POPULATIONS D'*APIS MELLIFICA* AVEC COUVAIN

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L'appareillage employé (logomètre, ruches, etc.) est le même que celui décrit dans ma précédente note concernant les mesures de température exécutées sur les ruches en hivernage (1).

Je vais d'abord parler de la constance thermique du couvain, de l'action de divers facteurs sur celle-ci ; et, enfin, ce qu'il faut penser de la présence du couvain dans les ruches en hiver.

A. — CONSTANCE THERMIQUE DU COUVAIN

Au cours de plusieurs expériences, nous avons enregistré la température en divers points de ruches peuplées possédant du couvain. Dans certains cas, nous avons opéré sur des colonies d'Abeilles faibles dont le couvain se réduit peu à peu jusqu'à la disparition de la colonie. Dans d'autres cas, les mesures ont porté toute une saison sur des colonies fortes, depuis le début de l'élevage jusqu'à la fin de l'automne.

Dans une colonie faible, le nid à couvain garde une température constante tant qu'il y a présence de quelques larves et malgré les variations thermiques parfois importantes du milieu ambiant (fig. 1). Cette température, aux environs de $+ 34^{\circ}$, n'est stable que dans les aires où le couvain est présent. Entre 2 rayons contenant du couvain, mais en dehors de la zone où il se trouve, la température est variable. La régulation thermique dans le couvain se fait d'une manière différente de celle du reste de la ruche. Dans le groupe d'Abeilles comme sur le plateau de sol, la courbe des températures n'est pas constante, elle se calque avec un certain retard et de moins grandes amplitudes sur celle de la température sous abri. Cependant il existe une régulation thermique en dehors du couvain puisque le sol de la ruche peuplée, par exemple, est plus froid par grandes chaleurs que le sol d'une ruche identique non peuplée. Les zones de couvain sont toujours restées à la même température à 1 ou 2 degrés près, bien que la tempéra-

(1) (L'enregistrement thermique continu dans les populations d'*Apis Mellifica* au cours de l'hivernage). *Insectes sociaux*, vol. 1, 1954.

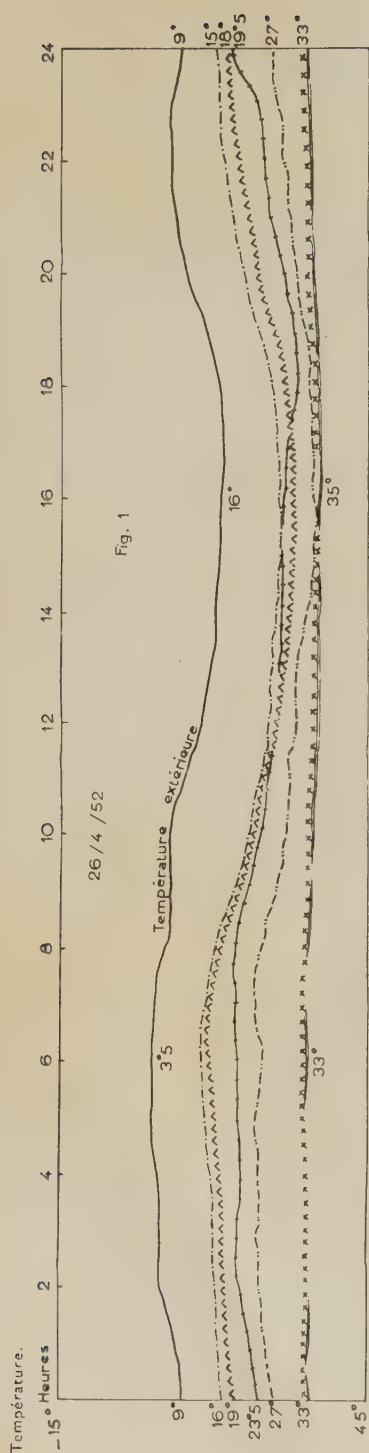


Fig. 1. — Température du couvain dans une ruche faible mettant en évidence la stabilité de celle-ci malgré les variations de la température extérieure.

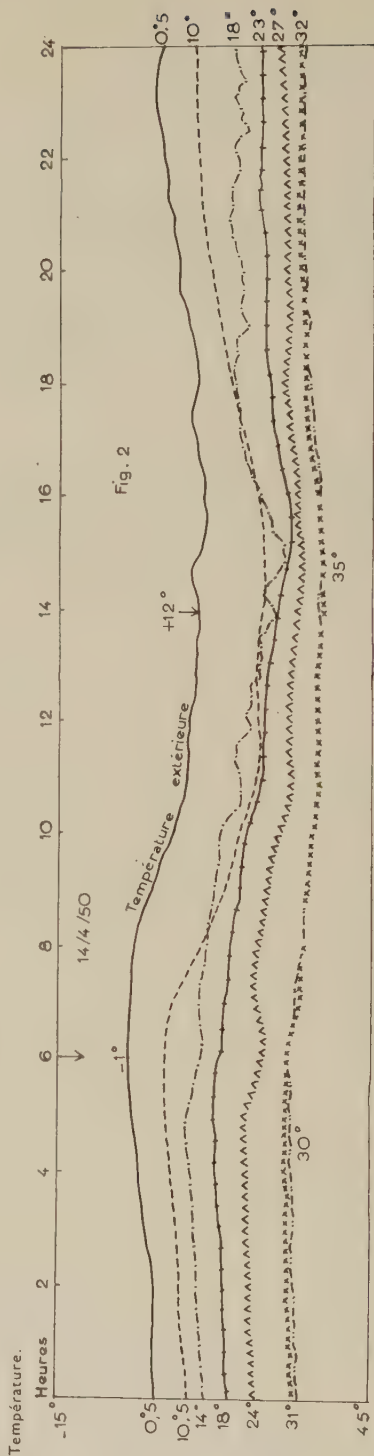


Fig. 2. — Température du couvain dans une ruche forte mettant en évidence la possibilité d'une variation journalière importante.

ture extérieure ait varié pendant les essais de -1° à $+20^{\circ}$. Par exemple, le 7 mars 1950, entre 8 heures et 17 heures, la température ambiante est passée de -1° à $+15,5^{\circ}$; le couvain, dans le même temps, a varié de $+33^{\circ}$ à $+35^{\circ}$. Lorsque le couvain disparaît dans une ruche, la courbe thermique de cette zone change d'allure en vingt-quatre heures. Par exemple, j'ai noté une baisse de 6° en vingt-quatre heures le 10 mars 1950; les jours suivants, la régulation en ce point est semblable à celle du groupe d'Abeilles sans couvain, la température n'y est plus constante. J'ai constaté l'absence du couvain lors de la visite complète de la ruche.

Dans les colonies fortes et normales, j'ai retrouvé les mêmes valeurs. Par exemple, des enregistrements effectués dans une ruche du 28 mars au 3 mai 1950 nous montrent la constance thermique du couvain entre $+30^{\circ}$ et $+35^{\circ}$, tandis que la température extérieure s'est étalée entre $+1^{\circ}$ et $+13^{\circ}$. Il peut se présenter cependant quelques différences journalières importantes; par exemple, le 14 avril 1950, à 5 heures, j'ai noté $+30^{\circ}$ dans le couvain et -1° sous abri météorologique, tandis qu'à 14 heures, le même jour, j'ai relevé $+35^{\circ}$ aux mêmes points et 12° à l'extérieur (fig. 2). La température dans le nid à couvain change donc assez peu; mais j'ai enregistré des variations plus importantes que celles signalées par Himmer et Hess, celles-ci pouvant atteindre plusieurs degrés en quelques heures.

A la fin de la saison d'élevage, les courbes correspondant au nid à couvain perdent leur régularité en quelques heures et varient dès ce moment, suivant la température extérieure, dans la même proportion que chez une ruche faible.

Il en est de même *au début de l'élevage*; dès qu'une ou plusieurs courbes thermiques prennent une allure presque régulière aux environs de $+32^{\circ}$ à $+33^{\circ}$, une visite de la colonie permet de trouver d'une manière certaine en ces points un peu de couvain.

D'autre part, j'ai fait des mesures thermiques dans le couvain d'une ruche très développée pour savoir si la température était la même dans le centre du nid à couvain et sur son pourtour. En faisant varier la position des sondes thermiques entre les cadres, il est facile d'enregistrer dans les diverses zones du nid à couvain. Des expériences nombreuses ont démontré qu'il n'existait aucune différence dans les diverses courbes enregistrées et que le pourtour du nid à couvain était doué comme le centre d'une stabilité thermique remarquable. Par exemple, pendant onze jours, la température ambiante ayant varié de $+8,5^{\circ}$ à $+25^{\circ}$, les courbes se sont toutes maintenues entre $+33^{\circ}$ et $+36^{\circ}$, quelle que soit leur position dans le couvain. En même temps, j'ai constaté une fois de plus que les mesures faites en dehors du couvain sont totalement différentes et sous la dépendance de la température extérieure.

B. — ACTION DE DIVERS FACTEURS SUR LA TEMPÉRATURE DANS LA RUCHE AVEC COUVAIN

Les journées très chaudes n'ont pas une grande influence sur la température dans le nid à couvain si elles ne surviennent pas brusquement. En juin 1950, les températures extérieures ont cependant atteint $+ 33^{\circ}$ sous abri ; dans les ruches situées au soleil, la courbe thermique du couvain montre exceptionnellement jusqu'à $+ 39^{\circ}$ maxima, tandis que, la nuit (minima environ $+ 10^{\circ}$), j'ai noté des valeurs de $+ 32^{\circ}$ dans ce même point. En dehors du couvain, parmi la population adulte, la température monte dans ces conditions jusqu'à des valeurs de $+ 40^{\circ}$ et même $+ 42^{\circ}$ (fig. 3). Depuis cette époque, nous n'avons jamais obtenu de telles valeurs pour la température dans le nid à couvain.

Par contre, un refroidissement brusque en dessous de $+ 10^{\circ}$, *même passager*, influe sur la température dans le couvain. Pour une température sous abri tombant de $+ 12^{\circ}$ à 0° les 11 et 12 avril, la courbe thermique du nid à couvain tombe de 34° à 29° . Ceci n'est d'ailleurs que de peu de durée puisque, le 14 avril, à 14 heures, la température atteignant $+ 12^{\circ}$, le couvain accuse alors $+ 34,5^{\circ}$. Il est sûr qu'un tel refroidissement cause un préjudice au développement des colonies, car, dans ce cas, un grand nombre de larves meurent.

J'ai enregistré, au cours des essais, l'effet produit par un orage. La température du nid à couvain s'était maintenue très près de $+ 33^{\circ}$ du 24 avril au 3 mai. Le 3 mai, entre 13 heures et 19 heures, la courbe monte jusqu'à $+ 36^{\circ}$. L'orage éclate vers 19 heures et la température revient assez rapidement à son ancienne valeur ($+ 33^{\circ}$ à 23 heures) et s'y maintient ensuite jusqu'au 15 mai. D'autres enregistrements ultérieurs m'ont donné les mêmes résultats. *Il existe donc une élévation de température, avant qu'un orage éclate, dans le nid à couvain d'une ruche* (fig. 4), *et il n'est pas nécessaire pour cela que la température extérieure augmente.*

Lors d'une désertion, la température augmente dans la ruche d'une manière très rapide (fig. 5). Le 19 mai 1950, j'ai noté les valeurs suivantes dans une colonie avant la désertion. La température sous abri a peu varié pendant ce temps.

A 9 h. 45, les divers points de la ruche sont entre $+ 19^{\circ}$ et $+ 21^{\circ}$, sauf dans le couvain.

A 10 heures, $+ 25^{\circ}$ partout, sauf le couvain.

A 10 h. 35, $+ 33^{\circ}$ partout.

A 10 h. 36, $+ 39^{\circ}$ et $+ 40^{\circ}$ dans tous les points de la ruche et jusqu'à 12 h. 30 environ.

Ensuite, la ruche étant dépeuplée, les courbes se calquent sur la courbe de la température sous abri.

Au mois de juillet, j'ai essayé de voir dans quelle mesure les courbes thermiques d'une colonie d'Abeilles étaient influencées par l'introduction de corps étrangers dans les ruches, les chocs et les visites de ruches. L'intro-

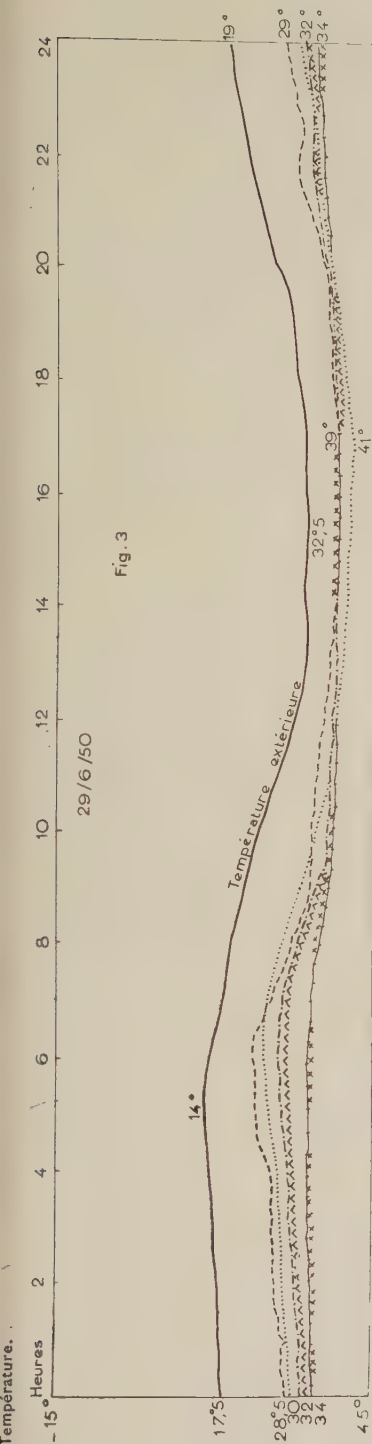


Fig. 3. — Influence exceptionnelle de la grande chaleur extérieure sur la température du nid à couvain.

— T° extérieure.

× × × × × × × T° dans le nid à couvain.

--- T° dans la ruche en dehors du nid à couvain.

..... T° dans la ruche en dehors du nid à couvain.

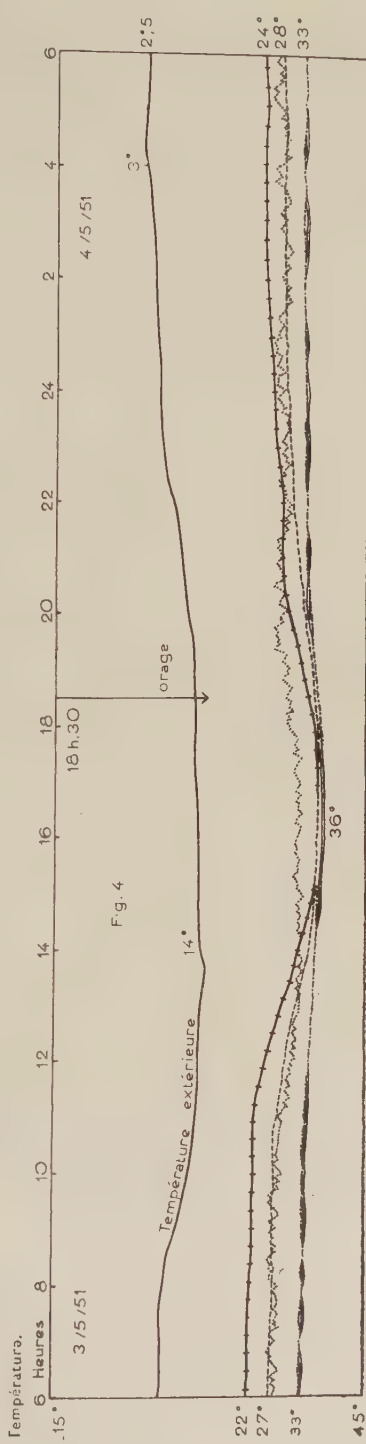


Fig. 4. — Influence de l'orage sur la température dans la ruche.

— T° extérieure.

× × × × × × × T° dans le nid à couvain.

--- T° dans la ruche en dehors du nid à couvain.

..... T° dans la ruche en dehors du nid à couvain.

duction d'une sonde métallique de 2 centimètres de diamètre et de 12 centimètres de long en n'importe quel point, par une température sous abri de $+ 23,5^{\circ}$ ne cause aucune perturbation dans l'allure des courbes thermiques de la ruche. Plusieurs coups de marteau très violents sur le toit

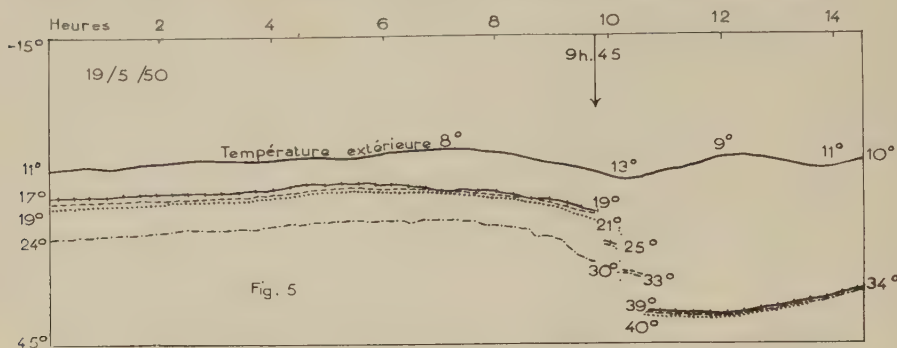


Fig. 5. — Enregistrement thermique dans une ruche lors de la désertion par les abeilles.

— T° extérieure ;
 - - - - - T° dans la ruche.

des ruches, par une température extérieure de $+ 25^{\circ}$, ne causent également aucun changement thermique.

La visite sommaire d'une ruche, pendant 1 mn 30 s, avec peu de

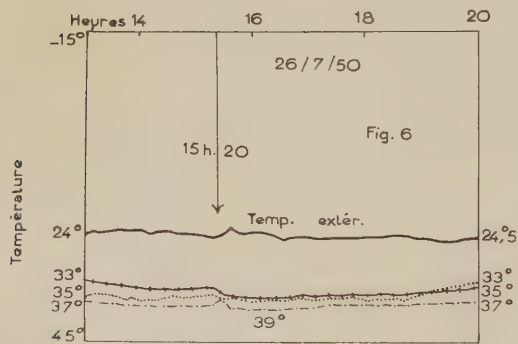


Fig. 6. — Enregistrement montrant qu'une visite de la ruche en été ne modifie pas la valeur de courbes thermiques de celle-ci.

— T° extérieure ;
 - - - - - T° dans la ruche.

fumée et la sortie d'un seul cadre pour contrôler la ponte, ne cause absolument aucune différence dans les courbes thermiques de la ruche. Je me suis alors demandé si la visite plus complète d'une colonie causerait un dérangement quelconque. J'ai sorti tous les cadres d'une ruche un par un avec un bon enfumage, par une température extérieure de 25° . Cette intervention a duré 6 minutes (fig. 6). Il n'y a pas eu de changement dans l'allure des courbes par la suite, sauf pendant l'ouverture de la ruche,

où les sondes furent enlevées. En résumé, je crois que le dérangement passager causé à une colonie avec couvain, en été, ne la perturbe pas au point de vue thermique. Il n'en n'est pas de même par une température plus froide au début du printemps, par exemple.

Nous avons été amené, au laboratoire, à pratiquer quelques claustrations

de ruches de diverses manières et, à cette occasion, j'ai enregistré la température dans ces colonies. Voici deux exemples : deux ruches sont claustrées sur hausse grillagée par-dessous et par-dessus le 12 mai 1952 au soir. La température monte seulement le 14 mai vers 6 heures ($+ 31^{\circ}$) à 42° à 14 heures, s'y maintient jusqu'à 17 h. 30 et retombe ensuite. Il y a eu dans l'intervalle mortalité importante, peu de nymphes vivantes et plus de couvain ouvert. Les abeilles sont libérées le 15 mai au soir et la ponte reprendra le 19 mai seulement. La température redevient normale dès l'ouverture des ruches. Une colonie est claustrée à nouveau par une simple toile métallique entre le corps de ruche et le plateau de sol le 15 juin à 21 heures, la température atteint $+ 41^{\circ}$ dans la nuit et le lendemain toutes les abeilles sont mortes, ainsi que le couvain.

C. — PRÉSENCE DU COUVAIN DANS LES COLONIES D'ABEILLES EN HIVER

Au cours de plusieurs enregistrements effectués en hiver, j'ai pu constater que certains points des ruches se maintenaient à une température variant entre 29° et 33° . Ces courbes étaient stables et cependant la température sous abri pendant ces mesures était très basse, parfois en dessous de 0° (même $- 5^{\circ}$). J'ai pensé qu'il pouvait y avoir dans ces colonies un peu de couvain. La visite des ruches en plein hiver lors de ces enregistrements a confirmé cette hypothèse. Il y a toujours dans ce cas présence de couvain dans la ruche, au moins quelques cellules. Je puis dire que, lors de ces interventions, il est très fréquent de rencontrer au moins une dizaine de cellules contenant du couvain. La reine continue sans doute de pondre d'une façon très ralentie. Ce point mériterait d'ailleurs une étude plus approfondie.

Résumé.

Les enregistrements thermiques continus m'ont permis de confirmer la constance de la température dans le nid à couvain :

1^o Du début à la fin de l'élevage ; 2^o dans les ruches faibles comme dans les ruches fortes ; 3^o dans les cadres du centre comme dans les cadres extrêmes du nid à couvain.

J'ai constaté cependant des variations journalières de cette constante thermique plus importantes que celles signalées jusqu'à présent.

J'ai mis également en évidence l'action de divers facteurs sur le comportement thermique de la colonie avec couvain : journées très chaudes, refroidissement brusque, orage, désertion, dérangement dans la colonie (visites ou chocs), claustrations.

Une grande constance thermique en hiver dans certaines colonies

d'Abeilles s'explique toujours par la présence de petites quantités de couvain.

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THE INCIPIENT COLONY OF *TENUIROSTRITERMES* *TENUIROSTRIS* (DESNEUX)

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Our knowledge of the development of the incipient termite colony is limited to a few species, primarily in the families *Kalotermitidæ*, *Hodotermitidæ* and *Rhinotermitidæ* (SNYDER, 1949). Almost nothing is known regarding the development of any species of the *Termitidæ*, especially those of the subfamily *Nasutitermitinæ*, having the distinctive nasute caste. The development of the young colony of *Tenuirostritermes tenuirostris* is, therefore, of particular interest especially since the number of young produced during early development of the colony is relatively large and includes a high proportion of nasutes (LIGHT and WEESNER, 1947) as compared with the small number of young and the limited soldier production in species of the lower families mentioned above.

MATERIALS AND METHODS

This study was carried out by the late Professor S. F. LIGHT with the assistance of the writer, during the summer and fall of 1946. The alates were obtained in Arizona from a group of colonies located at the mouth of Miller Canyon, on the south eastern slope of the Huachuca Mountains, in Cochise County. Alates obtained from under-rock workings as early as June 1 were sexually mature and showed the same pattern of colony development as did those alates obtained after normal emergence and flight on the evening of July 10. Only dealated individuals were used for pairing. In the case of alates collected from under-rock workings, dealation was induced by placing them in a cloth bag which was then sprayed with water.

A total of 466 pairs were set in culture between June 1 and July 18. The pairs were selected by sorting individuals on the basis of sternite structure rather than taking tandem pairs. Under laboratory conditions tandem pairs are not reliable since sometimes males follow males and females follow females. In mixed groups of alates, containing *Gnathami-*

termes perplexus (Banks), *Amitermes wheeleri* (DESNEUX) and *Tenuirostri-termes*, tandems were formed between dealates of different genera. BUCHLI (1950) also reports that in *Reticulitermes lucifugus* tandem pairs are not reliable.

The paired reproductives were maintained in five dram, screw-capped vials in various mixtures of agar-agar with soil and sawdust or with soil and dried grass cuttings. Of the original 466 pairs, 92 died within three days of setting. Forty of these initial deaths occurred in a group of sixty cultures set with a large proportion of sawdust. The others were distributed at random throughout the rest of the series. In general, the simple cultures of soil and agar-agar were the most satisfactory.

The records obtained were of two types, culture observations and census data. In the former, the young and eggs were observed in the undisturbed culture with the aid of a dissecting microscope. For some of these the records indicate the presence or absence of eggs or various types of young without any exact indication of number. In others, an attempt was made to indicate numbers, especially with respect to the early deposition of eggs and the initial appearance of young of various stages. Such counts became impractical as large numbers were involved. The critical data as regards total number of eggs or young are limited to census information obtained by removing the colonies from culture.

OBSERVATIONS.

A. Egg Deposition.

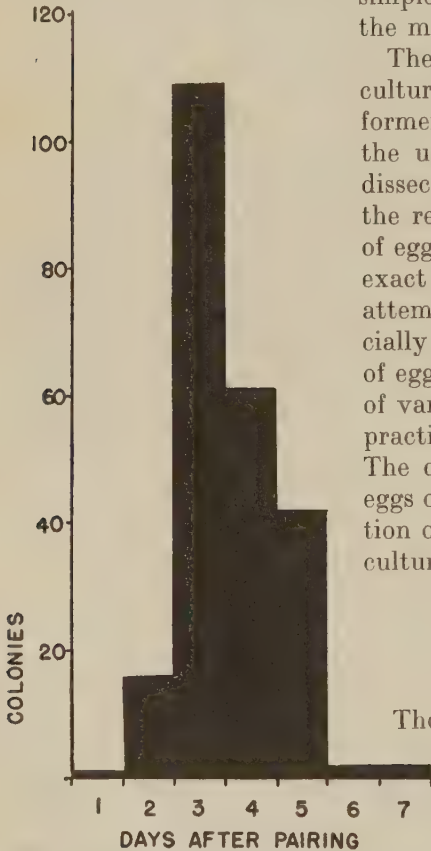


Fig. 1. — The initiation of egg laying in 233 colonies. Days after pairing refers to number of days which have elapsed since the pairs were placed in the culture vials.

The data on the initiation of egg laying (fig. 1) are limited to 233 of the surviving 374 pairs. These included cultures where the nuptial chamber was constructed next to the glass of the vial so that the eggs were readily observable. Of these 233 pairs, one, or 0.4 %, had deposited the first egg within 24 hours after pairing.

Sixteen colonies, or 6.8 %, deposited the first eggs on the second day; 109, or 46.7 %, on the third day; 61, or 26 %, on the fourth day; 42, or 18 %, on the fifth day, and two colonies, or 0.9 %, on the sixth and seventh days after pairing.

In 113 of these colonies a count was made of the eggs which were present, so that a fairly accurate picture of the rate of egg deposition is available. In addition, census data were obtained for egg production in 46 colonies which were removed from culture on the eighth, ninth and tenth days after pairing. In all but three of these latter, no previous record of egg

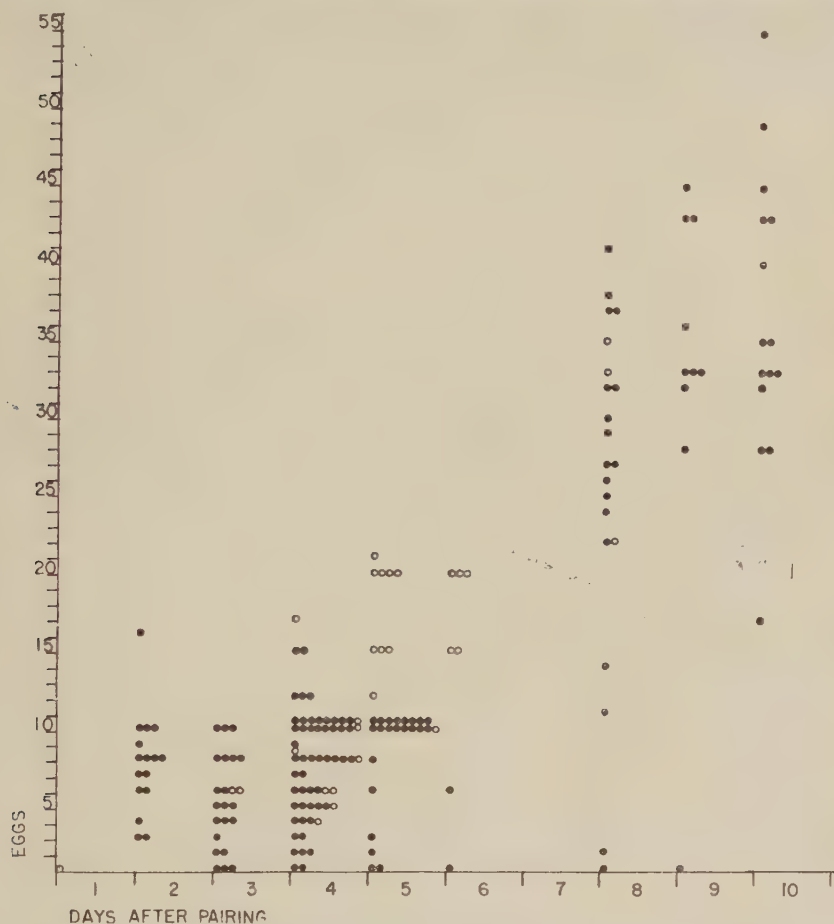


Fig. 2. — Egg production in 156 colonies during the first 10 days. Solid circles refer to initial observations of eggs within a particular culture. Open circles refer to subsequent observations. Data for the first six days after pairing are based upon counts in undisturbed cultures. Data for the 8, 9 and 10 days are based upon census information.

deposition was available since they were purposely selected from cultures where the workings were not maintained next to the glass. These counts indicate a remarkable rate of egg deposition (fig. 2). On the first day one egg was present in one colony and the maximum increased to 16 on the second day, 41 on the eighth day, 45 on the ninth day and 55 on the tenth day. It should be noted that a large number of eggs were observed in most of the colonies on the sixth and seventh days. These are not indicated

on the graph since their large number precluded an accurate count without census information.

No further census data were obtained until 30 days after pairing when 43 colonies were removed from culture. One of these had but five eggs and the remaining 42 had between 43 and 72 eggs with a mean of 61.0 eggs per pair. Subsequent data indicated that after the initial flare of egg production there is a decrease in the rate of egg laying and most eggs are deposited within 30 days. The maximum actual count was 76 eggs in a single culture. Almost all of the pairs produced at least 60 eggs during the initial egg laying period.

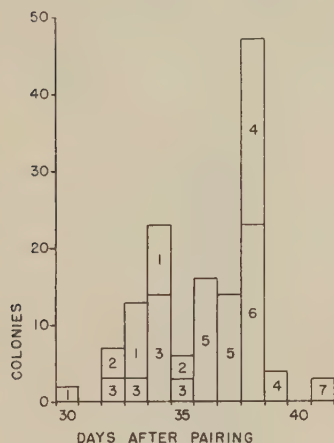


Fig. 3. — The appearance of young in 135 colonies. The figures in each column indicate the number of days which have elapsed between observations. Thus the first two colonies in which young were present on the thirtieth day have been examined on the twenty-ninth day. In the case of the 47 colonies in which young were first observed on the thirty-seventh day, 24 cultures had been observed four days earlier and 23 cultures had not been observed for six days. These young, therefore, might have actually been present as early as the thirty-fourth and the thirty-second day, respectively.

that the period of egg development must range from the observed minimum of 27 days to about 31 days.

B. *Development of the Eggs.*

The first young appeared in the colonies 30 days after pairing and 27 days after the first recorded appearance of eggs in those particular colonies. Figure 3 presents the available data on the appearance of young, utilizing only those records where the young which were present were still in the first stadium at the time of their initial observation. Since various colonies were examined at different time intervals, some adjustment must be made for the number of days which elapsed between observations. Thus, as indicated in figure 3, some colonies had been observed on the previous day and these are designated by the number 1; some two days earlier, designated by the number 2, and so. The general picture indicates that in most of the colonies the first young appeared between 30 and 35 days after pairing. When this is compared with the data on the initiation of egg laying (fig. 1) wherein most colonies had deposited the first egg by the third day after pairing, it is indicated

C. *The Individuals of the Incipient Colony.*

The preserved material available for a morphological study of the various instars of development was limited, but it did include representatives of

all types of young known to have been present during the development of the young colony. These types are comparable to those described for the worker and nasute lines in the mature colonies (WEESNER, 1953) although, with the exception of the first instar, the individuals of the incipient colony are consistently smaller.

Among the individuals of the incipient colony four types can be readily recognized with the unaided eye. These include the pigmented terminal individuals (the workers and the nasutes) and two unpigmented types.

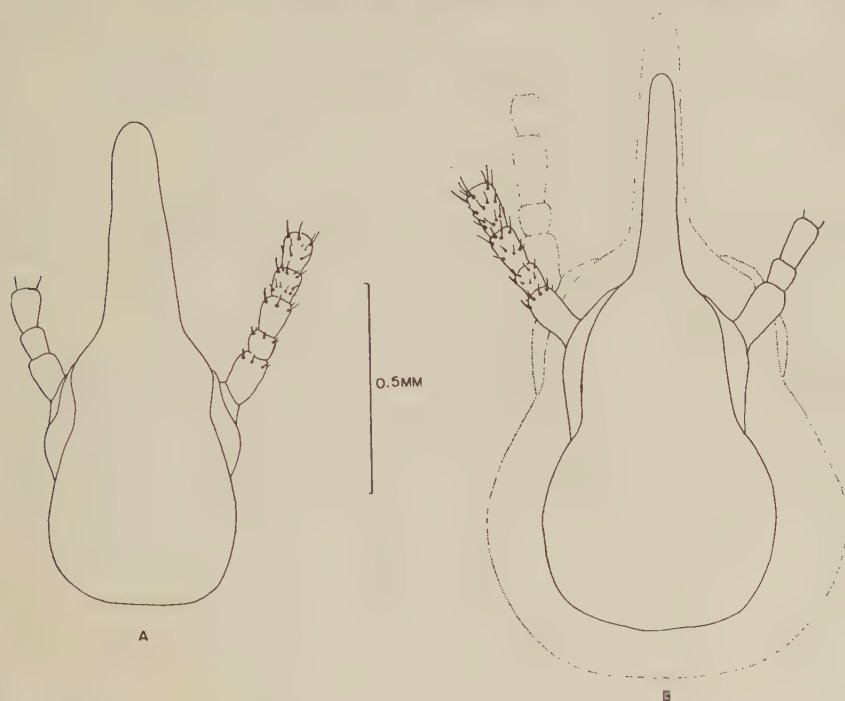


Fig. 4. — *a*, Head capsule of the nasute-nymph from the incipient colony. *b*, Head capsule of the nasute from the incipient colony (solid line) superimposed on the head capsule of a nasute from a mature colony (broken line). Camera lucida drawings.

One of these latter is the distinctive nasute-nymph with the elongated head (fig. 4, *a*). The second is the preworker stage, whose body and head size greatly exceeds that of the first instar or the young of the nasute line.

The distinction between the first instar young and the second and third instar young of the nasute line can be best defined on the basis of antennal structure. The structure of the antennae was found to be a simple and reliable guide in distinguishing the various instars of the mature group. In the following descriptions the antennal segments are numbered from the base. The basal segments are one and two and the flagellum begins with segment three.

The *first instar young* of the incipient colony show the same antennal

structure as those of the mature group. There are twelve antennal divisions of which the third and fourth are bare (lack bristles). The total length of the antennae is about 0.77 mm. The mean head breadth for thirty individuals was 0.50 mm, with a range from 0.48 to 0.53 mm. In one hundred first instar young from the mature colony the mean head breadth was 0.49 mm, with a range from 0.46 to 0.53 mm (WEESNER, 1953).

The *second instar nasute-line* individuals have 13 antennal divisions, as in the mature colony. In the case of the incipient individuals the third and fourth divisions are bare, whereas in comparable individuals from the mature group only the third lacks bristles. The total length of the antennae is 0.86 mm. For three individuals, adequately preserved for measurement, the head breadths were 0.50, 0.50 and 0.52 mm. In the mature colony the mean head breadth for 100 individuals of this type was 0.53 mm with a range from 0.50 to 0.55.

The *third instar nasute-line* individuals have 13 antennal divisions of which only the third is bare. The total length of the antennae is 1.06 mm. The mean head breadth for seven individuals was 0.52 mm, with a range from 0.50 to 0.53. This is distinctly less than that for comparable individuals from the mature colony where the mean for 100 was found to be 0.60 mm, with a range from 0.55 to 0.66 mm. In the mature group only the first individuals produced in the colonies each spring have 13 antennal divisions at this stage of development, later young having 14.

The *fourth instar nasute-line* individuals are the distinctive nasute-nymphs, having a definite anterior prolongation of the head (fig. 4, a). The antennal segmentation has been reduced to 12 segments. A comparable reduction of the segments occurs between the third and fourth instar young in the mature colony. The total length of the antennae has increased to 1.47 mm. The width of the head, as measured in five individuals, has not increased over that in the third instar young. In the mature colony there is a slight increase in head breadth between the third and fourth instar, 100 nasute-nymphs having a mean head breadth of 0.62 mm.

The nasute of the incipient colony is in the fifth stadium. There are 12 antennal segments and the head breadth of 20 individuals was found to range from 0.50 to 0.55 mm, with a mean of 0.53. This is distinctly less than the nasute from the mature colony where the mean for 100 individuals was 0.76 with a range from 0.71 to 0.81 mm. The relative size and proportions of the incipient and mature nasutes are shown in figure 4, b.

The *second instar worker-line* individuals can be distinguished from any of the nasute-line individuals on the basis of head size and antennal structure. They are, however, distinctly smaller than similar individuals from the mature colonies. Twenty incipient individuals of this stage had a mean head breadth of 0.72 mm, with a range from 0.69 to 0.76. One hundred individuals from the mature colony showed a mean head breadth of 0.82 mm, with a range from 0.77 to 0.88 mm. In individuals from both

the mature and incipient colonies there are 14 antennal divisions, all provided with bristles.

The incipient workers are in the third stadium. The mean head breadth for 46 individuals was 0.95 mm, with a range from 0.84 to 1.03 mm. In the mature colony, 100 workers had a mean head breadth of 1.14 mm, and ranged from 1.07 to 1.20 mm. Both incipient and mature workers have 14 antennal segments.

The period of time required for the development of the various instars of young has not been determined here, but certain statements can be made regarding the order of their appearance. The first observations of third-instar individuals of the nasute-line occurred prior to the appearance of second instar individuals of the worker-line. The nasute-nymphs appeared prior to the workers. Nasutes and workers appeared in most of the colonies within three days of each other. In some instances the nasutes appeared first and in other instances the workers. The initial appearance of nasutes and workers was on the fifty-ninth day after pairing. Allowing for the development of the eggs (27 to 31 days), the development through the four stadia of the nasute-line and the two of the worker-line requires about 28 to 32 days. These figures are in agreement with the development of the young in the mature colony where the minimum time for the appearance of the workers and the nasutes was found to be 28 to 30 days, respectively. It seems reasonable to conclude, therefore, that the developmental time of the various instars in each caste line in the incipient colony approaches the minimum developmental time observed for each in the mature colony.

It should be noted here that there was a continuous production of both nasutes and workers throughout the development of the incipient colony. Thus in a well-developed group, there would be present fully pigmented and callow workers and nasutes, as well as all stages of development in both caste lines.

D. *The Proportion of Nasutes and Workers.*

Critical data on the proportion of nasutes and workers is limited to 40 colonies which were censused at various times during the course of the study (fig. 5). Even these cannot be considered complete since in some instances the population had been reduced, probably by cannibalism, and in others the population was not fully developed as indicated by the presence of eggs and first instar young. Even admitting to considerable

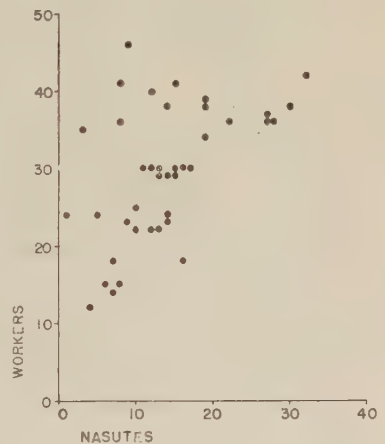


Fig. 5. — Numbers of nasutes and workers in 40 incipient colonies.

error, the data show a consistently high proportion of nasutes, which is usually in excess of 25 % of the total young present. The data would seem to suggest that the ratio of nasutes to workers probably approaches 1:2 rather than the more conservative estimate of 1:3. This is indicated by the high proportion of nasutes in the largest groups. Thus in the six largest colonies for which census data are available the numbers of nasutes and workers were found to be: 32 nasutes with 42 workers; 30 with 38 workers; 28 with 36; 27 with 37; 27 with 36, and 22 nasutes with 36 workers. The reduction of this ratio in smaller colonies would seem to be in agreement with the fact that cannibalism is apparently the main factor in reduction of the total population. Since individuals are most frequently cannibalized at the molt and the worker-line individuals experience only two molts as compared with four for nasuteline individuals, the greatest toll would be expected in the latter group.

DISCUSSION

The development of the incipient colony of *T. tenuirostris* exhibits several features which require further discussion. These include:

1. The rapid onset and high rate of egg deposition.
2. The production of a large number of eggs.
3. The production of many eggs and the rearing of the young, without any appreciable feeding on the part of the primaries.
4. The large number of defensive individuals (nasutes).
5. The continuous appearance of workers and nasutes, so that there is no indication that either are derived from a particular group of eggs or young.

With respect to the onset, rate and total of egg deposition, this species differs from those others for which data are available (see GRASSÉ, 1949, in *Traité de Zoologie*, for a summary of earlier work and the more recent paper of BUCHLI, 1950, on *Reticulitermes lucifugus*). The general pattern in the other species involves a delay of 15 or more days from pairing to the initiation of egg laying. This is followed by the production of less than 25 eggs over a period of 60 or more days with the eggs being deposited at intervals of a day or more. In a few instances there are records of an earlier onset and higher rate of egg production. Thus in *Coptotermes formosanus*, the first egg may be deposited on the fifth day and as many as one to four may be deposited daily.

The initiation and rate of egg deposition are indicative of the condition of the ovaries at the time of flight and/or the rate of yolk deposition in the oöcytes after flight. The immediate onset of laying in *T. tenuirostris*, indicates that some eggs are fully developed before the alates leave the parent colony. The rapid rate of deposition and the large total number may indicate either a limited production by a large number of functioning ovarioles, or rapid production from a few. An investigation of the

ovaries of young primaries of *T. tenuirostris* has shown that although 400 or more ovarioles are present in each ovary at the time of flight only six to eight are functional during the initial period of egg deposition. Each of these functional ovarioles contains four to six large, yolky eggs at the time the alate leaves the parent colony. The structure of the reproductive system will be reported more fully elsewhere.

The production of a large number of eggs and the rearing of the young without any plant food (or any indication of utilization of such food in the cultures where it was available) suggest large nutritive reserves at the time of flight. At the time of flight the fat bodies of the imagoes completely fill the abdomen and thorax, occupying all available space and greatly distending the body. The gut (as observed in sections) contains ligneous material and small quantities of soil. Subsequent to the deposition of the eggs the fat bodies are reduced although still extensive and conspicuous. When young are present in the colony the gut is found to contain considerable quantities of soil and even larger sand grains as well as extensive amounts of chitinous material. In most cases this latter probably represents the exuviae of the developing young although some cannibalism does occur. By the time the young colony has been reared, the fat bodies of the young pairs are extremely reduced and the flight muscles are almost completely resorbed. It would appear, therefore, that the primary nutritive source of the young colony is the fat reserve of the primaries and this is supplemented by the resorption of flight muscles and the ingestion of soil and cast skins as well as by some cannibalism.

In the *Termitidæ* as a whole, the nutrition of the incipient young is attributed to salivary feeding by the king and queen. Although this has not been demonstrated here it is indicated since there appeared to be stomadeal feeding and the salivary glands of the young pairs are tremendously developed. The immature individuals apparently did not ingest soil or plant material.

The large number of nasutes in the young colony is in agreement with the situation in the mature colonies. This portion of the developmental pattern is strikingly different from that described for the incipient colonies of the lower termites. In the latter, it has been shown that only one soldier is usually produced, although many, and probably all, of the initial young are capable of such development (CASTLE, 1934). While this first soldier is present it appears to inhibit the development of further soldiers until it is lost or the population size is increased beyond a critical point. If a similar mechanism functions in *T. tenuirostris*, the high production of defensive individuals might simply indicate a higher threshold of inhibition and the nasutes would be expected to appear first in the colony. This, however, is not the case, since both workers and nasutes appear continuously among the young.

In order to consider the pattern of colony development as it may effect the survival of the species, some mention should be made of the site of

colony foundation in the field, the behavior of the colonies in culture and the foraging habits of the species as observed in mature colonies. Young dealates of this species were found to excavate the nuptial chamber in the soil beneath surface rocks. Judging by the activities of young pairs in cultures, they do not appreciably extend the workings once the chamber has been excavated and the access passageway sealed off. As soon as the workers appeared, they extended a series of passageways through the soil of the culture and openings were made at one or several points in the surface of the culture mass. These activities in the laboratory groups are probably indicative of similar behavior in the field, with the extension of passageways from the nuptial chamber to the surface and the subsequent foraging for cuttings of weathered grass, as is the habit in the mature colonies. Since this species does not restrict its foraging activities to covered passageways, but moves above the surface of the ground, the problem of defense is extended from protection of a small opening in the workings to protection of completely exposed workers. The workers from mature colonies were accompanied on their expeditions by groups of nasutes and the same behavior might be expected of the incipient colonies.

It is indicated, therefore, that the rapid development of a large group of young may be correlated with the necessity of foraging for food and that such foraging activities must be initiated before the food reserves of the primaries are exhausted. The problem of foraging is not encountered in the wood-dwelling species which become established in their food source. Nor is it necessarily true for all subterranean forms, since many of these actually center their activities in wood. The large number of nasutes would appear to be correlated with the free-foraging activities of the workers which require a larger perimeter of defense than those species maintaining a closed system of workings.

Summary.

In *Tenuirostritermes tenuirostris* (DESNEUX) young queens usually initiate egg laying within four days after pairing. The initial rate of egg deposition is high, with as many as 55 eggs being deposited within the first 10 days. Between 10 and 30 days after pairing further eggs are deposited but at a reduced rate. Most of the young queens deposit at least 60 eggs by the thirtieth day and as many as 76 eggs were observed in a single culture. The eggs require about 27 to 31 days for development. The individuals from the incipient colony are comparable to those of the nasute-and worker-lines in the mature colonies. Only the first instar young can be considered common to both caste lines. The nasute-line includes three nasute-specific developmental stages, the last of which is the nasute-nymph. The nasute appears at the fourth molt. The worker-line includes a single worker-specific developmental stage, the

second instar. The worker appears at the second molt. With the exception of the first instar young, the incipient individuals are smaller than comparable individuals from mature colonies. The development through the two instars of the worker-line and the four instars of the nasute-line requires about 30 days from the time of hatching to the appearance of the terminal individuals. The percentage of nasutes present in the first group of young is in excess of 25 per cent and approaches 33 per cent in the largest groups. The nasute-line individuals do not appear to be derived from any particular group of eggs or young.

Zusammenfassung.

Junge Königinnen von *Tenuirostritermes tenuirostris* (DESNEUX) fangen gewöhnlich innerhalb von vier Tagen nach der Paarung an Eier zu legen. Im Anfang werden täglich viele Eier gelegt, bis zu 55 Eier innerhalb der ersten zehn Tage. Zwar werden auch zwischen dem zehnten und dreißigsten Tag nach der Paarung noch Eier abgelegt, aber in reduziertem Masse. Die Meisten der jungen Königinnen legen wenigstens 60 Eier bis zum dreißigsten Tage; es wurden aber bis zu 76 Eier in einer einzigen Kultur beobachtet. Die Entwicklung der Eier beansprucht ungefähr 27 bis 31 Tage. Die Individuen einer jungen Kolonie sind den „Nasenträger“- (nasute) and Arbeiter-linien der reifen Kolonien vergleichbar. Einzig die ersten Entwicklungsstadium-Jungen können als beiden Kasten gemeinsam betrachtet werden. Die „Nasenträger“-Linie umschließt drei „Nasenträger“-spezifische Entwicklungsstadien wovon das letzte Stadium die Nasenträger-Nymphe ist. Der eigentliche Nasenträger erscheint mit der vierten Häutung. Die Arbeiter Linie enthält ein einziges Arbeiter-spezifisches Stadium, das zweite Entwicklungsstadium. Der Arbeiter erscheint mit der zweiten Häutung. Mit der Ausnahme der Jungen im ersten Stadium sind die Individuen von jungen Kolonien kleiner als die vergleichbaren Individuen von reifen Kolonien. Die Entwicklung durch die zwei Stadien der Arbeiter-Linie und die vier der Nasenträger-Linie beansprucht ungefähr dreißig Tage vom Auschlüpfen des Eis bis zum endgültigen Stadium. In der ersten Gruppe von Jungtieren betragen die Nasenträger über 25 % und nähern sich in den größeren Gruppen einem Prozentsatz von 33 an. Die Nasenträger scheinen sich nicht von einer besonderen Gruppe von Eiern oder Jungtieren abzuleiten.

Résumé.

Chez *Tenuirostritermes tenuirostris* (DESNEUX), les jeunes reines commencent en général à pondre quatre jours après la parade. Le taux initial de ponte est élevé, il y a jusqu'à 55 œufs pondus pendant les dix premiers jours. Entre le dixième et le trentième jour après la fondation, d'autres

œufs sont encore produits, mais à une cadence réduite. La plupart des jeunes reines ont alors pondu au moins 60 œufs, le maximum observé étant 76. Le développement des œufs demande vingt-sept à trente et un jours. Les individus de la jeune colonie sont comparables à ceux des lignées conduisant aux ouvriers et aux *nasuti* des colonies adultes. Seul, le premier stade est apparemment commun aux deux lignées. La lignée des *nasuti* comporte trois stades intermédiaires spécifiques, le dernier étant le soldat-blanc ; le *nasutus* apparaît à la quatrième mue. La lignée des ouvriers comporte un seul stade intermédiaire spécifique, le deuxième stade ; l'ouvrier apparaît à la seconde mue. A l'exception des jeunes du premier stade, les membres de la jeune société sont plus petits que leurs équivalents des colonies adultes. Le développement (deux stades pour la lignée des ouvriers, quatre stades pour celle des *nasuti*) demande environ trente jours de l'éclosion à l'apparition des individus terminaux. La proportion de *nasuti* dans les individus issus de la première couvée dépasse 25 p. 100 et approche 33 p. 100 dans les sociétés les plus peuplées. Les insectes de la lignée des *nasuti* ne semblent pas dériver d'un groupe particulier d'œufs ou de jeunes larves.

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UNTERSUCHUNGEN ZUR METAMORPHOSE DER HONIGBIENE (*Apis mellifica* L.)

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EINLEITUNG

Schnürungsversuche an Metamorphosestadien von Insekten bieten eine sehr einfache Methode, die Abgabeorte von Stoffen, die für das Häutungs-geschehen wichtig sind, grob zu lokalisieren. Aus der Entwicklung der abgeschnürten Körperteile kann auf die Funktion von ausgeschalteten Organen geschlossen werden. Der exakte Nachweis der hormonellen Bedeutung für Häutung und Metamorphose wurde durch Exstirpations- und Re- Implantationsexperimente geführt für die neurosekretorischen Zellen des Gehirns, die Corpora cardiaca, die Corpora allata und die Prothoraxdrüsen, während eine Unterbindung nervöser Impulse zu dieser Zeit bedeutungslos war.

Es zeigte sich dabei, daß die Corpora allata und Prothoraxdrüsen als Antagonisten den Charakter der Häutung und die Auslösung der Metamorphose bestimmen. Zusammenfassungen dieses Problems finden sich bei PIEPHO (1951, 1952), SCHARER (1952, 1953).

Bei der Honigbiene sind die gleichen vier Arten von Drüsen vorhanden. Sie entwickeln sich in der gleichen Weise und zeigen zu den gleichen Entwicklungszeiten Sekretionsercheinungen, an denen bei anderen Insekten die kritische Periode experimenteller Beeinflussung liegt. LUKOSCHUS (1952, 1954).

Erste hormonphysiologische Untersuchungen an der Bienenlarve wurden von L'HÉLIAS (1951) und SCHALLER (1951, 1952) beschrieben. Nach L'HÉLIAS sollen Organe des Kopfes die totale Metamorphose bewirken. Bei den Folgerungen, die die Autorin aus ihren Schnürungsversuchen zieht, muß jedoch berücksichtigt werden, daß ihr das Vorhandensein einer Prothoraxdrüse bei der Biene noch nicht bekannt war (LUKOSCHUS, 1952) und daß sie auf einer Literaturangabe von BORDAS et JANET (1893) fußt, nach der in der Entwicklung der Biene lediglich zwei Larvenstadien vorhanden sein sollen.

Andererseits berichtet SCHALLER von einem Ueberspringen des Puppenstadiums bei der geschnürten Larve, statt seine Versuchstiere unter dem Gesichtspunkt der Reaktion der Hypodermis auf das 2-Hormonsystem (KÜHN und PIEPHO, 1938; PIEPHO, 1951) zu betrachten. Die von SCHALLER und L'HÉLIAS ausgesprochenen Folgerungen lassen sich mit den Ergebnis-

sen gleicher Schnürungsversuche an anderen Objekten nicht vereinbaren.

Bei einer größeren Reihe von Insektenarten verschiedener Ordnungen traten bei den Versuchen die gleichen Erscheinungen, Häutung und Metamorphose betreffend, auf. Es zeigte sich dabei, daß die Wirkung der Sekrete homologer Drüsen art-, gattungs- und ordnungs-unspezifisch war (PIEPHO, 1950).

Auch die Drüsen der Honigbiene wirken in der gleichen Weise artunspezifisch auf den Wirt wie die homologen Drüsen anderer, genauer untersuchter Objekte (THOMSEN, 1943; KOLLER, 1948).

Es kann nun erwartet werden, daß bei der Biene Hormon-Drüsen, die gleiche Veränderungen im Häutungszyklus zeigen wie die anderer Insekten, die gleiche, bei allen untersuchten Arten festgestellte Bedeutung für Häutung und Metamorphose besitzen.

Bei dem heutigen Stand unserer Kenntnis von der Hormonphysiologie der Metamorphose bei Insekten konnte darauf verzichtet werden, durch Exstirpations- und Re- Implantationsexperimente die Drüsen als Hormonbildungsstätten auch bei der Biene zu identifizieren.

Ziel dieser Arbeit ist es daher :

1. Die Bedeutung der in den Körperabschnitten grob lokalisierten Inkretdrüsen für die Metamorphose festzustellen,
2. Die kritischen Perioden festzulegen.

Damit sollen vergleichbare hormonphysiologische Grundlagen für Untersuchungen über die Entstehung des weiblichen Dimorphismus bei der Honigbiene geschaffen werden.

MATERIAL UND METHODE

Die Untersuchungen wurden durchgeführt an Arbeiterinnen von *Apis mellifica carnica* Pollmann und an Königinnen von allen im Landesinstitut für Bienenforschung in Celle gehaltenen Zuchtschmümmen.

Die Heranzucht des Untersuchungsmaterials erfolgte mit den in der deutschen imkerlichen Praxis weitverbreiteten Methoden nach ZANDER (1953).

In Voruntersuchungen zeigte sich, daß die Metamorphose der Biene mit geringeren zeitlichen Schwankungen abläuft, als es von anderen Insekten her bekannt ist. Dies ist eine Folge der gleichmäßigen Fütterung und der konstanten Temperatur-Bedingungen im Brutnest des Bienenstockes. Wenn man also in kurzen Zeitabständen Tiere entnimmt, erhält man lückenlose Reihen aufeinander folgender Entwicklungsstadien.

An Stelle morphologisch ablesbarer Entwicklungszustände [Augenklassenreihe KÜHN u. PIEPHO (1938), STELLWAAG (1954)] gibt bei der Biene also schon eine zeitliche Datierung genau reproduzierbare Entwicklungsstadien.

Es ist dabei jedoch notwendig, die gesamte Entwicklungszeit mehrfach zu unterteilen, da die von mehreren Autoren durchgeführte tägliche Ent-

nahme nach der Eiablage nicht zu ausreichend genauen Ergebnissen führen kann. Als leicht fassbare Entwicklungsstadien wurden daher das Schlüpfen der Made aus dem Ei, die Verdeckelung der Zellen durch die Arbeiterinnen und die Puppenhäutung (genauer das Abstreifen der Larvenexuvie) benutzt. Es hat sich dabei gezeigt, daß die Zellverdeckelung durch die Pflegebienen sehr genau den Anfang der Vorpuppenzeit und damit den eigentlichen Beginn der Metamorphose anzeigt. Von diesem Zeitpunkt an verläuft die Metamorphose sehr gleichmäßig.

Eine auf $\pm 1 \frac{1}{2}$ Stunden genaue Zeitdatierung war für die Untersuchungen ausreichend. Diese wurden in der folgenden Weise durchgeführt :

Larven : Bestiftete Waben wurden mit der Uhrmacherlupe auf das Schlüpfen der Eimaden kontrolliert. Zellen mit frischgeschlüpfter Made erhielten eine Farbmarkierung an der Zellwand.

Vorpuppen : Bei Waben mit geschlossenem Brutnest älterer Maden wurde das Verdeckeln durch die Pflegebienen beobachtet. Die Farbmarkierung erfolgte auf dem Zelldeckel.

Puppen : Zellen mit Streckmaden wurden entdeckelt und die Waben im Thermostaten bei 35°C aufbewahrt. Der Zeitpunkt des Abstreifens der Exuvie war dabei leicht festzustellen.

Die vorsichtige Entnahme der Versuchstiere aus ihren Wabenzellen erfolgte stets erst vor der Schnürung, um Entwicklungsschocks zu vermeiden. Die Schnürungen wurden an folgenden Stellen durchgeführt :

Vorpuppen :

a. Hinter dem 1. Thoraxsegment.

Anlegen der Ligatur hinter dem nicht sehr festen Kopfkapsel hat bei fortgeschrittenen Entwicklungsstadien oftmals ein Zurückrutschen des Gehirns und der anhängenden Drüsen hinter die Schnürung zur Folge.

b. Hinter dem 3. Thoraxsegment.

Diese Körperstelle wurde gewählt, weil eine Abschnürung hinter dem 1. Segment bei der weichhäutigen Bienenlarve ein Zurückrutschen des Darmes und der Prothoraxdrüsen hinter die Ligatur zur Folge hat. Selbst ohne Verschiebungen des Körperinhaltes würde bei einer weiter vorn liegenden Schnürung ein Teil der bis in den Metathorax hineinreichenden Prothoraxdrüse in den abgeschnürten Hinterkörper gelangen. Siehe Abb. 1.

Die Befunde von L'HÉLIAS müssen unter diesem Gesichtspunkt betrachtet werden.

Puppen :

a. Zwischen Kopf und Thorax ;

b. In der Wespentaille.

Die Schnürungen unter a werden im Folgenden als „Kopfschnürung“, die unter b als „Thoraxschnürung“ bezeichnet.

Die geschnürten Tiere wurden auf Kokonunterlage (der Länge nach hal-

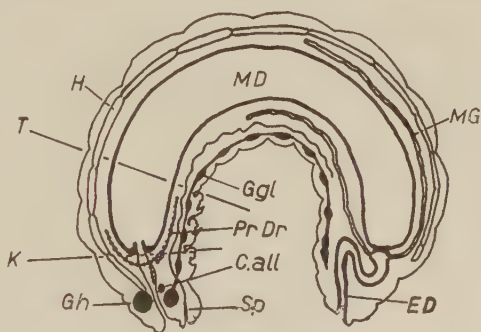


Abb. 1. — Schematischer Schnitt durch die Bienenlarve.

C. all., Corpus allatum; Ed., Enddarm; Gh., Gehirn; H., Herzschlauch; K., Kopfschnürung; Md., Mitteldarm; MG., Malpighi-Gefäße; Pr. Dr., Prothoraxdrüse; Sp., Spinndrüse; T., Thoraxschnürung.

bierten Königinzellen) in Plexiglasschalen im Thermostaten bei 35° C aufbewahrt.

Fixiert wurde nach BOUIN, ALLEN, BAUER bei 40° C unter Benutzung eines leichten mit der Wasserstrahlpumpe erzeugten Vakuums.

Bei Stadien mit fortgeschrittener Inkrustierung war eine Behandlung mit Chlordioxyd - Salpetersäure erforderlich.

Nach Paraffineinbettung wurden 7 1/2 μ dicke Serienschritte hergestellt. Diese wurden mit Hämatoxylin nach HEIDENHAIN gefärbt. Für die Darstellung des Aufbaues der Cuticula war eine Gegenfärbung mit Benzolichtbordeaux vorteilhaft.

Kopfschnürung	25 25 5 3 9 1	n	Dauerlarven
	100 100 100 80 13 4	n	Zwischenformen
	2 41 13 2	n	Puppen
Thoraxschnürung	40 58 54 25	n	Dauerlarven
	20 10 6 14 6 2 8	n	Zwischenformen
	29 42 75 100 100 100 100	n	Puppen
	22 37 10 12 12 12	n	Dauerlarven
	100 100 67 40 14	n	Zwischenformen
	2 2 3 1	n	Puppen
	4 16 70 18 18 7 5 4	n	Dauerlarven
	22 53 82 95 100 100 100 100	n	Zwischenformen
	22 53 82 95 100 100 100 100	n	Puppen
Schnürungstermin in Stunden nach der Verdeckelung			
0 8 12 16 24 30 36 42 48 54 60			
Verlassen des Putters Spinnbeginn			
letztes Kötchen Sekretionserscheinungen Kampferperiode Spinnende			
Plasmaausscheidung der Epidermiszellen			
Cuticulablädung Sekretionserscheinungen der Corp. cardica			
Entwicklungsstadien			

Tabelle 1. — Schnürungsversuche an Arbeiterinorpuppen. Beobachtung der Hinterkörper. 448 Ueberlebende.

DIE ENTWICKLUNG DES ABDOMENS DER GESCHNÜRTE ARBEITERIN

Bei den datierten Arbeiterinnen, bei denen in der oben angegebenen Weise Schnürungen durchgeführt wurden, wurden die in den Tabellen 1 und 2 zusammengefaßten Ergebnisse erhalten. Die Beurteilung der Versuchstiere erfolgte zum Zeitpunkt der Imaginalhäutung der Kontrollen.

Bei Kopfschnürungen sind an bekannten Hormonbildungszentren ausgeschaltet: die neurosekretorischen Zellen des Gehirns, die Corpora cardica und die Corpora allata. Bei Thorax-

Tabelle 2. — Schnürungsversuche an Arbeiterinorpuppen. Beobachtung der Hinterkörper. 471 Ueberlebende.

Kopfschnürung	n	Dauerpuppen
	n	Zwischenformen
	70 62 54 31 52 20	n	Imagines
Thoraxschnürung	47 36 27 20 34 18	n	Dauerpuppen
	100 100 100 100 100 100	n	Zwischenformen
	n	Imagines
Schnürungstermin in Stunden nach der Puppenhäutung			
0 12 24 36 48 60 72			
Puppenhäutung			
Mitosenperiode			
Plasmaausscheidung der trichogenen Zellen und Epidermiszellen			
Cuticulablädung			
Entwicklungsstadien			

schnürungen sind ausser den genannten Drüsen auch die Prothoraxdrüsen nicht im Hinterkörper vorhanden. Aus der Entwicklung der Hinterkörper,

die durch Schnürungen zu verschiedenen Entwicklungszeitpunkten von den Drüsen abgetrennt wurden, soll auf die Funktion dieser Drüsen geschlossen werden.

Es ist dabei übersichtlicher, die Verhältnisse während der Puppenzeit zuerst zu analysieren.

DIE IMAGINALDIFFERENZIERUNG

Die Bedeutung des Thorax. — Das vom Kopf abgeschnürte Puppenhinterteil entwickelt sich in jedem Falle, auch bei Schnürung im Zeitpunkt der Puppenhäutung, imaginal weiter. Das vom Thorax abgeschnürte Abdomen zeigt keine weiteren Differenzierungen. Daraus ist zu schließen, daß stoffliche Faktoren aus dem Thorax für die Imaginalausbildung erforderlich sind.

Im Thorax sind nun an Drüsen, die als Entstehungsorte dieser Faktoren in Frage kommen könnten, nur die Prothoraxdrüsen vorhanden.

Da sie zu der gleichen Zeit Sekretionserscheinungen zeigen, ist es wahrscheinlich, daß die Differenzierungsfaktoren des Thorax mit den Sekreten der Prothoraxdrüse identisch sind.

Dies steht in Übereinstimmung mit den Befunden an vielen anderen Objekten. Zusammenfassung bei SCHARRER (1952). Danach ist die Imaginaldifferenzierung abhängig von Hormonen der Prothoraxdrüse und nicht von Faktoren des Kopfes, wie L'HÉLIAS annimmt.

Die Bedeutung des Kopfes. — Bei frühen und späten Terminen während des Puppenstadiums ist bei Kopfschnürungen kein Unterschied in der Ausbildung der Hinterkörper festzustellen. Der Kopf ist für die Imaginaldifferenzierung im Puppenstadium nicht mehr notwendig.

Bei Kopfschnürungen der späten Streckmade (42-60 Stunden nach der Verdeckelung) jedoch erfolgt die Puppenhäutung in der normalen Weise. Es findet keine Weiterentwicklung in imaginaler Richtung statt, obwohl im Hinterkörper die Prothoraxdrüse vorhanden ist.

Daraus ist zu schließen, daß ein Faktor aus der Kopfregion zu einem frühen Zeitpunkt für die Imaginaldifferenzierung erforderlich ist. Dieser Faktor wirkt nicht selbständig, sondern nur im Zusammenwirken mit dem Thorax. Thoraxschnürungen zu einem viel späteren Zeitpunkt in der Puppenzeit verhindern die imaginale Ausbildung.

Die histologischen Befunde von Sekretionserscheinungen in den neurosekretorischen Zellen des Gehirns und in den Corpora cardiaca zu diesem Zeitpunkt (LUKOSCHUS, 1954) lassen vermuten, daß die Sekrete dieser Drüsen mit den Kopffaktoren identisch sind.

Die zeitliche Trennung der kritischen Perioden läßt eine Relaiswirkung Kopf- Thorax- Imaginaldifferenzierung vermuten.

Diese Befunde entsprechen denen bei einer Anzahl von Objekten. Zusammenfassung bei PIEPHO (1951,1952), SCHARRER (1952). Danach

scheiden die neurosekretorischen Zellen des Gehirns auf dem Wege über die Corpora cardiaca ein prothoracotropes Hormon aus.

Die kritische Periode des Kopfes für die Imaginaldifferenzierungen liegt vor der Puppenhäutung. Es entspricht dies den Befunden an *Tenebrio* (STELLWAAG, 1954) und *Bombyx* (BOUNHIOL, 1952).

Die kritische Periode des Thorax für die Imaginaldifferenzierungen kann nicht genau erfaßt werden. Selbst wenn in der Puppe die Schnürung erst erfolgt, wenn imaginale Bildungsvorgänge bereits eingesetzt haben, wie Abscheidung der Exuvialflüssigkeit, Mitosenperiode, Heranwachsen der trichogenen Zellen, Auswachsen der Plasmafortsätze der trichogenen Zellen und sogar Beginn der Bildung der Cuticula, zeigt sich in dem vom Thorax abgeschnürten Teil keine Versteifung der Sklerite (die früher als Inkrustierung beschrieben wurde) und keine Pigmenteinlagerung. Die Pigmentierung als die letzte und am leichtesten zu fassende Differenzierung der imaginalen Cuticula (sie ist durch die transparente Puppencuticula hindurch mit bloßem Auge leicht erkennbar) benötigt auch in späten Entwicklungsstadien das Vorhandensein von Faktoren aus dem Thorax. Von einer deutlich abgesetzten kritischen Periode, von der an die Entwicklung autonom verläuft, kann also nicht gesprochen werden. Dies steht in Übereinstimmung mit Befunden an vielen Objekten. Zusammenfassung SCHARRER (1952).

Danach ist das Sekret der Prothoraxdrüsen von Bedeutung für den Aufbau des imaginalen Cytochromsystems. Dieses wirkt über die Tyrosinase auf die Pigmentierung des imaginalen Chitins ein.

DIE PUPPENHÄUTUNG

Die Bedeutung des Thorax. — Bei Thoraxschnürungen der Streckmade (ab 30 Stunden nach der Verdeckelung) erfolgt Ablösung der Larvencuticula, Abscheidung der Exuvialflüssigkeit, Bildung der Puppencuticula und Einsetzen von Häutungsbewegungen auf beiden Seiten der Ligatur.

Bei Schnürungen der frühen Spinnmade (bis 12 Stunden nach der Verdeckelung) findet eine Weiterentwicklung zur Puppe nur im abgeschnürten Vorderteil statt.

Danach ist die Puppenhäutung abhängig von Faktoren des Vorderkörpers. Zu dieser Zeit (15-30 Stunden nach der Verdeckelung) sind im histologischen Bild Sekretionserscheinungen der Prothoraxdrüsen und der Corpora allata festzustellen (LUKOSCHUS, 1952, 1954). Nach diesem Zeitpunkt histologisch sichtbarer Sekretabsonderung dieser Drüsen erfolgt die Weiterentwicklung im abgeschnürten Hinterkörper autonom. Dieser Zeitraum (20-25 Stunden nach der Verdeckelung) kann als Beendigung der kritischen Periode für die Puppenhäutung angesprochen werden.

Die physiologischen Daten „Beendigung des Kotens und Spinnen des Innenkokons“ lassen einen Vergleich mit der kritischen Periode anderer Objekte zu.

Die Bedeutung des Kopfes. — Bei Kopfschnürungen der jungen Spinnmade (bis 12 Stunden nach der Verdeckelung) erfolgt keine Weiterentwicklung zur Puppe. Die kritische Periode liegt ebenfalls wie bei dem Thoraxfaktor im Zeitraum 20-25 Stunden nach der Verdeckelung.

Sekretionserscheinungen in den neurosekretorischen Zellen des Gehirns (L'HÉLIAS, 1951) und eigene histologische Befunde von Sekretvakuolen in den Corpora cardiaca lassen vermuten, dass der Kopffaktor mit diesen Sekreten identisch ist.

Dies würde in Uebereinstimmung stehen mit den Befunden an einer Reihe von Objekten. Zusammenfassung bei SCHARER (1952).

Die kritischen Perioden des Kopfes und des Thorax fallen zusammen. Die mit einer Häutung verbundene Weiterentwicklung beträgt im Zeitraum :

	6	12	18	24	30	36	STUNDEN NACH DER VERDECKELUNG.
bei Kopfschnürung	0	40	87	96	100		%
bei Thoraxschnürung	0	33	60	86	100		% der Ueberlebenden

Aus den Zahlenunterschieden zwischen Kopf- und Thoraxschnürung kann bei dem vorliegenden Material kaum auf eine Zeitspanne zwischen den kritischen Perioden geschlossen werden.

In Analogie zu den besprochenen Verhältnissen während der Entwicklung zur Imago ist jedoch zu vermuten, dass — wie bei anderen Insekten auch, — die Puppenhäutung nicht von Faktoren des Kopfes direkt ausgelöst wird, sondern auf dem Wege über die Prothoraxdrüse.

Das 2-Hormonsystem und der Charakter der Häutung.

Durch Kopfschnürungen von Spinnmaden entstehen in größerer Anzahl die als Zwischenformen bezeichneten Versuchstiere. Bei diesen findet man unter der sich abhebenden Larvenexuvie z. T. inkrustierte und pigmentierte Abdomina. Sie erinnern weitgehend an die Verhältnisse bei der Imago. Im histologischen Bild einiger nur teilweise pigmentierter Objekte zeigt die Cuticula sämtliche Uebergänge zwischen pupaler und imaginaler Differenzierung. Eine durch Häutungs Vorgänge abgehobene Puppencuticula fehlt in allen Fällen.

Die wenigen auch bei Thoraxschnürungen erhaltenen Zwischenformen sollen hier nicht weiter berücksichtigt werden. Es erscheint möglich, daß sie durch das Zurückgleiten von Teilen der Prothoraxdrüse hinter die Ligatur entstanden sind.

Früh geschnürte Spinnmaden zeigen weitgehend imaginale Differenzierungen (Abb. 2, *a*, *b*). Spätere Schnürungstermine ergeben pupale Objekte mit kleinen Bereichen imaginaler Differenzierungen (Abb. 2 *c*). Noch spätere lassen nur pupale Merkmale erkennen.

Die erhaltenen, abweichend differenzierten Objekte sind pupal-imaginale Zwischenformen. Sie sind mit den protelen Formen zu vergleichen, die bei Ausschaltung der Corpora allata, bzw. bei deren Unterfunktion entstehen (WIGGLESWORTH, 1947; KÜHN, 1948; WEBER, 1949).

Die histologischen Befunde von Sekretionerscheinungen bei den Corpora allata und bei den Prothoraxdrüsen in diesem Zeitraum der Normalentwicklung machen wahrscheinlich, daß das durch die Schnürung gestörte Mengenverhältnis der Hormone zueinander die Ursache für die gefundene abweichende Entwicklung ist.

Bei frühen Schnürungsterminen haben die neurosekretorischen Zellen des Gehirns noch nicht das Hormon abgeschieden, das die Prothoraxdrüse zur Sekretion anregt. Es findet keine Weiterentwicklung statt. Zu einem späteren Schnürungszeitpunkt, wenn dieser Anstoß bereits erfolgt ist, die Sekretion der Prothoraxdrüsen aber noch nicht eingesetzt hat, befinden sich im abgeschnürten Hinterkörper die autonom sich weiter entwickelnde Prothoraxdrüse und sehr geringe Mengen Corpora allata-Hormon. Es entwickelt sich ein weitgehend imaginal differenziertes Abdomen.

Zu einem noch späteren Zeitpunkt hat die Sekretion der Corpora allata bereits eingesetzt. Im abgeschnürten Hinterkörper befinden sich die bis zu diesem Zeitpunkt abgeschiedenen Mengen Corpora allata-Hormons und die Prothoraxdrüse, die ihre ganze Sekretmenge in den Hinterteil abgibt. Es entwickeln sich Abdomina, die pupal-imaginalen Zwischenformcharakter zeigen.

Bei einem Schnürungszeitpunkt, an dem die Sekretion der Corpora allata bereits erfolgt ist, ist im abgeschnürten Hinterkörper die fast normale Menge Corpora allata-Hormon vorhanden und die Normalmenge des ebenfalls bereits abgeschiedenen Prothoraxdrüsenhormons. Es entstehen normale Puppenabdomina. Diese entwickeln sich nicht weiter zu Imagines, da hierzu ein erneuter Anstoß seitens der Drüsen des Kopfes erforderlich ist.

Diese Befunde stehen in Übereinstimmung mit der Lehre vom 2-Hormon-system (WIGGLESWORTH, 1940; PIEPHO, 1941). Danach wird der Charakter der Häutung durch das Mengenverhältnis der Hormone aus den Corpora allata und der Prothoraxdrüse bestimmt. Große Mengen Corp. all.-Hormons geben der kommenden Häutung den Charakter einer Larvenhäutung (Jugendhormon), geringere Mengen den einer Puppenhäutung, und sehr geringe Mengen oder das Fehlen von Corp. all.-Hormon bewirken durch das Ueberwiegen der Prothoraxdrüse eine Imaginalhäutung.

Die Zwischenformen.

Die durch Schnürungen der Spinnmaden erhaltenen Zwischenformen sind verschieden weit in imaginaler Richtung abgewandelt. Bei Betrachtung

tung der Ausdehnung der imaginalen Sklerite, der Inkrustierung und der Pigmentierung können die Versuchstiere zu einer gleitenden Zwischenformenreihe von pupal bis weitgehend imaginal zusammengestellt werden (Abb. 2).

Aus den Ausbildungsbereichen der imaginal abgewandelten Cuticula muß auf das gleiche Gefälle cranial nach caudal und dorsal nach ventral geschlossen werden, wie es PIEPHO (1946) bei Teilverpuppungen und Larven-Puppen-Zwischenformen bei Schmetterlingen beschrieben hat. Während der Metamorphose vollzieht sich der Uebergang der primären Segmentie-



Abb. 2. — Dorsalansichten von *Abdomina proteler* pupal-imaginaler Zwischenformen.
a—d : Abnahme imaginaler Merkmale (Inkrustierung, Pigmentierung, sekundäre Segmentierung).

rung der Larve zu den dachziegelartig übereinandergreifenden Skleriten, dem äußeren Anzeichen der sekundären Segmentierung der Imago. Hierbei erfolgt in der Normalentwicklung die Verkürzung des Abdomens, bei der die Körpersegmente der Larve sich teleskopartig ineinanderschieben. Der Stachelapparat wird in das Körperinnere eingezogen und damit die Oligomerie des weiblichen Hymenopterenabdomens hergestellt. Bei den Zwischenformen unterbleibt die sekundäre Segmentierung weitgehend, die Einziehung des Stachelapparates in allen Fällen.

Die Cuticula und die Epidermisbildungen zeigen Abweichungen von der Norm der pupalen und der imaginalen Ausbildung, die gesondert beschrieben werden sollen.

Die Entwicklung des Vorderkörpers bei der geschnürten Arbeiterin

Bei Thoraxschnürungen der Vorpuppen entwickelt sich der Vorderkörper in jedem Falle weiter. Abscheidung der Exuvialflüssigkeit, Herausbildung der pupalen Form der Körperanhänge und beginnende Ausfärbung

pigmentiertes Insekt aus der Wabenzelle. Die Königin verläßt die Zelle in der Regel als vollausgebildetes Insekt verschieden lange Zeit nach der Imaginalhäutung.

Für eine vergleichende Betrachtung werden Verlassen des Futters und Imaginalhäutung als entwicklungsphysiologische Daten verwendet :

	KÖNIGIN.	ARBEITERIN.
Vorpuppenzeit, d. h. Verlassen des Futters-Puppenhäutung	60	85 Stunden,
Puppenzeit, d. h. Puppenhäutung-Imaginalhäutung	120	190 Stunden.

Königin und Arbeiterin weisen bei gleichen äußeren Bedingungen vergleichbare Entwicklungsleistungen auf. Die Temperaturverhältnisse, die bei der Königin sogar ungünstiger erscheinen, sollen später behandelt werden. Die Unterschiede in der Entwicklungszeit lassen vermuten, daß bei der Königin ein stoffwechselstimulierender Faktor vorhanden sei.

Nach den Befunden an anderen Objekten wird der Gesamtstoffwechsel durch die Corpora allata beeinflußt (THOMSEN, 1942, 1949; DAY, 1943). Dabei wurde der Sauerstoffverbrauch als Ausdruck des Gesamtstoffwechsels gemessen. Bei weiteren Objekten wurde eine Korrelation von Stoffwechselintensität und Corpora allata-Volumen und-Sekretion festgestellt (WILLIAMS, 1946; KAISER, 1949; SCHWINCK, 1951).

Auch bei der Biene sind die Corpora allata der Königin mit der kurzen Entwicklungszeit groß, die der Arbeiterin mit der langen Entwicklungsdauer klein.

Wenn die Annahme zu Recht bestünde, daß auch bei der Biene die Stoffwechselintensität von den Hormonen der Corpora allata beeinflußt wird, dann müßte Stoffwechselintensität und Hormonmenge in gesetzmäßigem Zusammenhang stehen.

Messungen des O_2 -Verbrauches und der CO_2 -Abgabe während der larvalen und pupalen Entwicklung von Königin und Arbeiterin wurden von MELAMPY und WILLIS (1939) durchgeführt.

Ihre in der Abbildung 3 eingezeichneten Kurven zeigen :

1. Allgemein höhere Werte bei der Königin.
2. Die Abnahme in der Metamorphose der Königin ist relativ und absolut größer als bei der Arbeiterin.
3. Der Anstieg in der Puppenzeit ist bei der Königin wesentlich stärker als bei der Arbeiterin.

Die gleichen Grundzüge konnten in der Volumenentwicklung der Corpora allata festgestellt werden (LUKOSCHUS, 1954). Die Mittelwerte eines größeren Materials (185 Königinnen und 158 Arbeiterinnen) sind in der Abbildung in Kurvenform eingetragen.

Eine Gegenüberstellung von Sauerstoffverbrauch und Corpora allata-Volumen zeigt in allen Punkten vollständige Korrelation, wenn man berück-

sichtigt, daß die Volumenverringerung der Corpora allata während der späten Vorpuppenzeit auf Sekretabgabe nach Beendigung der Sekretproduktion zurückgeführt wurde (Abb. 3). Danach ist es wahrscheinlich,

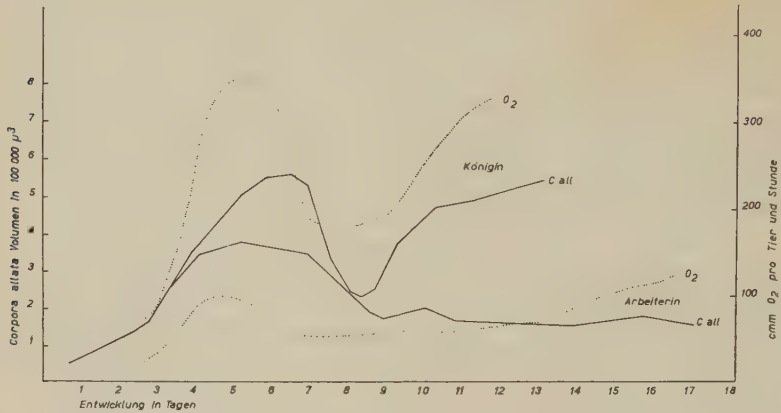


Abb. 3. — Corpora allata-Volumen und Sauerstoffverbrauch während der Entwicklung von Königin und Arbeiterin. Sauerstoffverbrauch nach MELAMPY u. WILLIS (1939).

daß die vergrößerten Corpora allata und der intensivere Stoffwechsel der Königin die schnellere Entwicklung, eine Kasteneigentümlichkeit, verursachen.

Die Befunde bei den Schnürungsversuchen zeigen, daß durch die verhinderte Verbreitung von Faktoren aus den Kopfregionen Bedingungen geschaffen werden, die denen bei der Königin angenähert sind. Es ist zu vermuten, daß diese Faktoren mit den Hormonen der Corpora allata identisch sind.

Schnürungsversuche an Königinnen.

Bei Königin-Vorpuppen und -Puppen wurden in der gleichen Weise wie bei der Arbeiterin Kopf- und Thoraxschnürungen durchgeführt.

Von 417 geschnürten Tieren überlebten 132.

Die hohe Sterblichkeit der Versuchstiere ist wahrscheinlich auf nicht erkannte Schädigungen zurückzuführen, welche die Königinnenlarven während des Transportes von den teilweise entfernten Außenständen erlitten hatten.

Die bei der Arbeiterin an größerem Versuchsmaterial aufgezeigte Abhängigkeit der Metamorphose von Faktoren des Kopfes und des Thorax gilt auch bei der Königin. Zwischenformen bei der Kopfschnürung der Spinnmade traten jedoch nicht auf.

Besprechung der Ergebnisse.

Schnürungsversuche, die als methodisch einfachste Änderung des Hormonsystems angesehen werden können, beeinflussen die Entwicklung der Honigbiene in der gleichen Weise, wie es von anderen Insekten berichtet wird. Durch diese Schnürungen entstehen die gleichen inkrustierten und pigmentierten imagoähnlichen Formen, die L'HÉLIAS und SCHALLER bei ihren Versuchen erhalten haben. Eine genauere Beobachtung der Metamorphose läßt jedoch nicht die Folgerungen zu, die diese Autoren aus den Versuchen ziehen.

Entgegen L'HÉLIAS liegt die kritische Periode, wie es auch SCHALLER beschreibt, in der Spinnmadenzeit und entspricht somit den Verhältnissen bei anderen Insekten.

Vergleichbar den Ergebnissen bei zahlreichen Arten ist der Charakter der Häutung von Faktoren des Kopfes und des Thorax abhängig und nicht von Faktoren des Kopfes allein. Die erhaltenen Zwischenformen müssen als protele Bildungen angesprochen werden, bei denen die Puppenhäutung in verschieden starkem Masse in imaginaler Richtung abgewandelt ist.

Ähnlich den Versuchen über die Abhängigkeit der Stoffwechselintensität von den Hormonen der Corpora allata (THOMSON, 1949; DAY, 1943) tritt bei Kopfschnürungen im Hinterkörper eine Verzögerung der Entwicklung ein, bei Thoraxschnürungen im Vorderkörper eine Beschleunigung. SCHALLER beobachtete die verzögerte Entwicklung im Hinterkörper bei seinen Kopfschnürungen. Er nahm an, daß die Puppenhäutung übersprungen werde und die sich bildende Cuticula die normale Imaginal-Cuticula sei. Aus dem Zeitpunkt der Pigmentierung der Versuchstiere schloß er auf eine Entwicklungsbeschleunigung, die der Entwicklungsgeschwindigkeit der Königinnen entspräche.

Diese Folgerung würde in Widerspruch zu den gesicherten Erkenntnissen über die Stoffwechselabhängigkeit von Hormonen stehen (Zusammenfassung bei SCHARRER, 1952).

Wenn man aber beachtet, daß die fragliche Häutung eine verzögerte, in imaginaler Richtung abgewandelte Puppenhäutung ist und nicht eine vorzeitig erfolgende imaginale Häutung, löst sich der Widerspruch.

Nach diesen Versuchen ist es sehr wahrscheinlich, daß die Metamorphose bei der Honigbiene in der gleichen Weise wie bei anderen Insekten von Hormonen gesteuert wird.

Die bei den Angehörigen der Kasten aufgetretenen Unterschiede in der Größe und in der Sekretion der Hormondrüsen lassen vermuten, daß eine Beziehung zwischen ihnen und den während der Metamorphose ausgebildeten Kastenmerkmalen besteht. Untersuchungen über die Bedeutung des inkretorischen Systems für die Herausbildung von Kastenmerkmalen bei Honigbienen sollen an anderer Stelle beschrieben werden.

Meinem verehrten Lehrer, Herrn Prof. Dr. *H. Piepho*, danke ich für die Anregung zu dieser Arbeit. Die Versuche wurden im Sommer 1952 im Niedersächsischen Landesinstitut für Bienenforschung und bienenwirtschaftliche Betriebslehre in Celle durchgeführt, dessen Direktor Herr Dr. *Wohlgemuth* die Arbeit durch die Heranzucht von Königinnen in großen Mengen ermöglichte. Fräulein *Ursula Sievert* danke ich für wertvolle technische Hilfe bei der Durchführung der Versuche.

Zusammenfassung.

Es werden Schnürungsversuche an Larven und Puppen von Honigbienen beschrieben. Aus den Ergebnissen ist zu folgern :

1. Auslösung und Durchführung der Metamorphose sind bei der Biene in der gleichen Weise wie bei anderen Insekten von stofflichen Faktoren abhängig.

2. Bildungszentren dieser Faktoren sind wahrscheinlich Prothoraxdrüsen, Corpora allata und neurosekretorische Zellen des Gehirns.

3. Die imaginale Differenzierung ist abhängig von Faktoren des Thorax. Störungen im 2-Hormon-System führen zur Bildung proteler, pupal-imaginaler Zwischenformen.

4. Die Stoffwechselintensität ist abhängig von Faktoren des Kopfes.

Résumé.

Ce rapport décrit des expériences de ligatures pratiquées chez la larve et la nymphe d'abeille. Les conclusions suivantes nous semblent justifiées :

1. Chez l'abeille, la détermination et le déroulement de la métamorphose dépendent de facteurs humoraux, de même manière que chez les autres insectes.

2. Les centres d'origine de ces facteurs sont probablement les glandes prothoraciques, les corpora allata et les groupes de cellules neuro-sécrétrices.

3. Des dérangements dans le système des 2-hormones causent la formation des types intermédiaires, particulièrement des chrysalides-imaginales précoces.

4. L'intensité de l'assimilation dépend de facteurs céphaliques.

Summary.

Ligature experiments on larvae and pupae of honeybees are described. We can conclude from the results the following :

1. Determination and performance of the metamorphosis depend — with bees in the same way as with other insects — on humoral factors.

2. The centres of origin of these factors are probably the prothoracic glands, the corpora allata, and the neurosecretory cells of the brain.
3. The imaginal differentiation depends on thoracic factors. Derangements in the 2-hormon-system lead to the formation of premature adultoids.
4. The intensity of metabolism depends on factors of the head.

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UNTERSUCHUNGEN AN EINER PARASITISCHEN AMEISE (*Anergates atratulus* SCHENCK)

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(Aus dem Institut für Angewandte Zoologie der Universität Würzburg, Vorstand :
Prof. Dr. K. Gößwald.)

I. EINLEITUNG

Anergates atratulus SCHENCK ist eine Ameise, bei der die Arbeiterkaste fehlt, also nur noch Geschlechtstiere vorhanden sind. Die Aufzucht der Brut wird von den ♀♀ einer anderen Ameisengattung übernommen, in deren Nest *Anergates* lebt. *Anergates* ist, da Ameisen zu den staatenbildenden Insekten, die auch soziale Insekten genannt werden, gehört, Sozialparasit bei *Tetramorium caespitum* L., einer nahe verwandten Art. Wie haben also eine besondere Form von Parasitismus vor uns, die mit der Adoption des ♀ einer anderen Gattung in einem fremden Ameisenstaat beginnt. Da sich bei Ameisen der einzelne Staat, d. h. jedes Nest durch einen besonderen „Nestgeruch“ auszeichnet, müssen bei Sozialparasiten besondere Bedingungen erfüllt sein, die eine Adoption ermöglichen (s. GÖßWALD, 1938, und MEYER, 1951). Von entscheidender Bedeutung ist außer anderen Faktoren die Weisellosigkeit des Wirtsameisenstaates. Das in diesem Zusammenhang interessierende Problem der stammesgeschichtlichen Entwicklung des Ameisenparasitismus wurde besonders von GÖßWALD (1933, 1934, 1938 und 1951) behandelt. Demnach stehen *Anergates* und noch mehr die erst kürzlich entdeckte *Teleutomyrmex schneideri* Kutter, die bei demselben Wirt lebt, am Ende der heutigen Entwicklungsreihe. Die letztere Ameise wurde von GÖßWALD (1953) histologisch untersucht und mit *Anergates* verglichen.

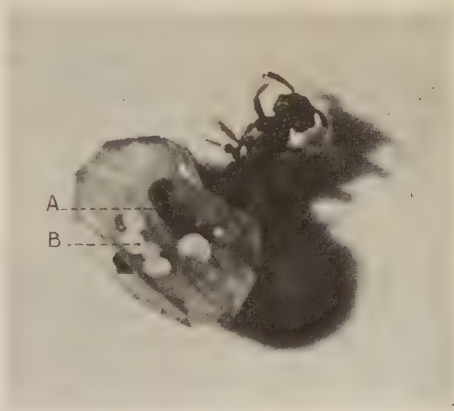


Abb. 1. — *Anergates* ♀, physogaster.
A = Tergit, B = Eier.

2. HABITUS DER GESCHLECHTSTIERE

Das ♀ ist wie bei anderen Ameisen geflügelt, das ♂ dagegen flügellos, mit nach ventral eingekrümmtem Abdomen. Es ist auffallend pigmentarm (Beschreibung bei ADLERZ, 1887, STITZ, 1939). An Stelle der Flügel finden sich mikroskopisch kleine Flügelrudimente (ANDRÉ, 1885, und DONISTHORPE, 1927). Die Flügeladerung der ♀♀ zeigt eine auffallende Variationsbreite, die terminologisch zumindest verschiedenen Arten entsprechen würde und auf eine genetisch labile Situation bei *Anergates* hinweist.

Bedingt durch die Flügellosigkeit der ♂♂ findet ausschließlich Begattung zwischen Geschlechtstieren desselben Nestes statt (Adelphogamie). Durch reine Inzucht kann es also zu einer weiteren Anreicherung degenerativer Anlagen kommen.

3. HISTOLOGIE

Im folgenden sollen einige besondere histologische Veränderungen, die in Zusammenhang mit der parasitischen Lebensweise stehen, besprochen werden (Einzelheiten s. MEYER, 1951).

a) **Darm.** — Während der Bau des Darmtrakts beim ♀ keine auffallenden Besonderheiten zeigt, ist der Mitteldarm des Männchens merkwürdig verändert. Das Epithel ist manchmal flach wie bei Ameisenlarven und besitzt dann keine Regenerationsnester. Häufig fehlt jedes Anzeichen einer Sekretion, manchmal sezerniert die eine Hälfte holokrin, während die andere völlig funktionslos erscheint. Da in manchen Fällen Regenerationsnester fehlen, wird durch eine solche einmalige holokrine Sekretionswelle das Mitteldarmepithel zerstört. Es kommt beim ♂ also nicht in allen Fällen zur Ausdifferenzierung eines funktionsfähigen, imaginalen Mitteldarms. Wahrscheinlich nehmen die ♂♂ im Verlauf ihrer kurzen Lebenszeit keine Nahrung auf und sterben nach einer mehrmaligen Kopula, wenn der Spermiovorrat erschöpft ist.

b) **Drüsen.** — Die Kopfdrüsen sind beim ♀ durch die paarigen Mandibular- und Pharyngealdrüsen vertreten, dagegen fehlt die Maxillardrüse, die bei *Tetramorium* vorhanden ist. Die unpaare Labialdrüse ist bis auf wenige Drüsenzellen im Thorax zurückgebildet und hat häufig keinen Ausführgang mehr. Manchmal fehlt sie ganz. Entsprechend sind die Verhältnisse beim ♂.

c) **Muskulatur.** — Auch die Muskulatur des ♂ zeigt sowohl topographisch wie histologisch degenerative Veränderungen. Im Thorax wird die Flugmuskulatur nicht mehr angelegt. Offensichtlich wird das dort befindliche Fett von der Larve in die Puppe bzw. Imago übernommen.

Im Vergleich zu *Tetramorium* ist im Querschnitt die zentrale Sarkoplasmasäule verbreitert (auf ungefähr $\frac{1}{3}$ bis $\frac{1}{2}$ des Gesamtdurchmessers der Muskelfaser). Die Verteilung der Kerne ist häufig unregelmäßig, neben kernarmen Partien kommen lokale Anhäufungen vor. Offensichtlich ist der Muskel aber trotzdem noch funktionsfähig.

d) **Nervensystem.** — Besonders eindrucksvoll zeigt sich die Auswirkung des Parasitismus am ZNS von *Anergates* ♂♂ und ♀♀. Allgemein werden die *Corpora pedunculata* als Zentren höherer, associativer nervöser Funktionen bei Insekten betrachtet. Sie sind besonders beim ♂ sehr klein, und weisen oft keine Becher mehr auf, sondern nur noch eine knollige Anhäufung von Ganglienmasse. Die Stiele lassen sich häufig nicht mehr trennen. Die Lobi optici bestehen nur noch aus wenigen Fasern, dagegen sind die drei Ocelli durch relativ dicke Faserbrücken mit dem Protocerebrum verbunden. Sie erscheinen besser innerviert als die Komplexaugen. Beim ♂ und beim ♀ ist das Deutocerebrum gut entwickelt.

Zum ersten Male konnten bei Insekten «tigroide» Ganglienzellen nachgewiesen werden, die meist in Gruppen zusammenliegen. Sie finden sich nur in der Puppe. Die Nisslsubstanz ist in Form von Schollen und größeren Granula im Neuroplasma angehäuft. Die Anordnung in Gruppen deutet auf einen Zusammenhang mit mitotischen Vorgängen. Zusätzlich wird die Ribosenukleinsäure der Schollen wahrscheinlich beim Auswachsen des Zellfortsatzes verwertet. Da sich die Nisslsubstanz nur während der Puppenruhe bildet, muß ihr eine Bedeutung bei der Histogenese des Nervensystems zukommen. Neben motorischen Ganglienzellen werden auch assoziative (z. B. Globuli) tigroid. Die sich hier äußernde physiologische Aktivität der Nervenzellen erinnert sehr an Vorgänge bei Warmblütern (vergl. LANDSTRÖM, CASPERSSON UND WOHLFAHRT, 1941. und C. und O. VOGT, 1946).

Zwischen den Nisslschollen treten ebenfalls nur in der Puppe Vakuolen im Neuroplasma auf. Ihr Inhalt ist weder mit basischen noch mit sauren Farbstoffen färbbar.

e) **Die Haut.** — Die Cuticula des ♂ macht einen larvalen Eindruck ohne deutliche Gliederung. Dagegen zeigten Vergleiche zwischen *Anergates*-♀ und anderen Ameisenarten (*Tetramorium*-♀ und *Formica rufibarbis*-♀),

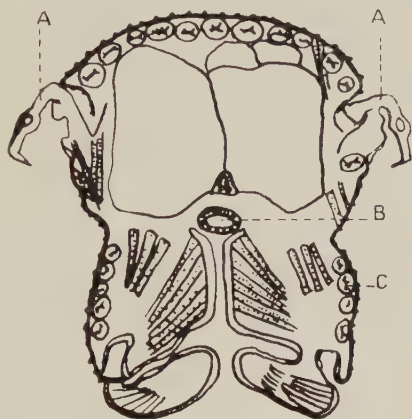


Abb. 2. — *Anergates* ♂, Thoraxquerschnitt, vereinfacht.

Vergr. 60 fach.

A = Flügelrudimente, B = Esophagus, C = Fettzellen.

daß eine Abgrenzung von Exo- und Endocuticula schwierig ist. Auch hier erweist es sich als zweckmäßig, beide Schichten zusammenzufassen (vergl. WIGGLESWORTH, 1948, und WEBER, 1952), und als primäre Endocuticula zu bezeichnen. Die Epicuticula ist bei den untersuchten drei Arten in vergleichbarer Dicke vorhanden, lediglich beim *Anergates*-♂ ist sie nicht sicher zu erkennen.

f) **Der Stachelapparat.** — Im Gegensatz zu Angaben von ADLERZ (1887), der bei den von ihm untersuchten Tieren einen Stachelapparat vorfand, hatten die ♀♀ des Würzburger Gebietes keinen solchen mehr. Vielleicht sind einige tubulöse Drüsen zwischen Sphinkterabschnitt und Vagina als rudimentäre Giftdrüse zu deuten.

g) **Pericardialzellen.** — Nach WEBER, 1952, kommen außer den typischen, als Nephrocyten betrachteten Pericardialzellen und sog. Phagocytärorganen auch solche mit innerer Sekretion vor. Hierher gehören die Pericardialdrüsen der Insekten.

Bei *Anergates* sind sie im Larvenstadium stark vakuolisiert und ohne sichtbare Zellgrenzen. Sie wachsen bei älteren Larvenstadien heran, während der Kern pseudopodienartige Fortsätze in das Cytoplasma entsendet. Diese Oberflächenvergrößerung des Kernes deutet auf eine besondere physiologische Aktivität. In der Puppe nimmt das Zellvolumen wieder ab und ist imaginal am kleinsten. Auffallend ist, daß sich die Zellen kurz vor der Verpuppung im dorsalen Raum verteilen, d. h. die Verbindung zum Rückengefäß aufgeben. Während dieser Zeit ist das Cytoplasma außerdem stark basophil.

h) **Innere Geschlechtsorgane.** — Obwohl zahlreiche Individuen in Kopula histologisch untersucht werden konnten, war trotzdem kein lückenloser Einblick in die histo-physiologischen Vorgänge zu erreichen. Die Hoden bestehen aus drei Follikeln und zeigen dieselben Bauverhältnisse wie sie n'ROZARIO (1942) bei anderen Hymenopteren beschrieb. Bei *Anergates* müssen die Spermien die Anhangdrüse passieren. Diese besitzt ein hohes zylindrisches Epithel mit basal gelegenen gelappten Kernen. Das Sekret wird im apikalen Teil der Zelle gespeichert. Es fließt im allgemeinen vor der Kopula nicht aus, d. h. das Lumen der Drüse ist meist frei von Sekret. Während der Kopula waren die Hoden stark geschrumpft, die Samenblasen voll von Spermien. Obwohl an der Uebergangsstelle von der Samenblase zur Anhangdrüse kein Verschlußapparat zu erkennen ist, finden sich erst Spermien — von einzelnen wenigen Fällen abgesehen — nach Zerstörung der Zellwände des hohen Zylinderepithels und Freiwerden des Sekretes im Lumen der Anhangdrüse. Sie zeigen dann lebhaftere Bewegungsformen, während sie in den Samenblasen gebündelt und ausgestreckt liegen. Der Spermienvorrat reicht für mehrere Kopulationen, da offensichtlich in der Zwischenzeit eine Reifung weiterer Spermienelemente im Hoden möglich ist.

Beim ♀ liegen zwischen Vagina und Rektum außer den schon beim Stachelapparat beschriebenen Drüsen andere Drüsenzellen mit Ausführungsgang, die von JANET (1902) bei *Myrmica rubra* nicht beschrieben wurden.

Das Receptaculum weist eine Anhangdrüse ektodermaleer Herkunft auf. Die Spermien werden wohl chemotaktisch an das Receptaculum herangeführt, in dem sie sich ordnen und wiederinaktiviert, d. h. bewegungslos werden. Einige wenige wandern aber auch am Receptaculum vorbei direkt in die Ovidukte. Zur Befruchtung muß dann wieder eine Aktivierung der aus dem Receptaculum entlassenen Spermien stattfinden. Histophysiologische Beweise für die Produktion verschiedener Stoffe zur Inaktivierung und Aktivierung der Spermien konnten nicht erbracht werden. Die Ovarien flottieren frei in der Leibeshöhle, sind also nicht mit einem Terminalfilum fixiert.

i) **Die Physogastrie.** — *Anergates*-♀♀ und *Teletomyrmex*-♀♀ zeigen wie die bekannteren Termiten-♀♀ postmetabole Veränderungen, die mit ihrer großen Fertilität zusammenhängen. Außerlich



Abb. 3 — *Lasius niger-alienus* ♀, replete Form.

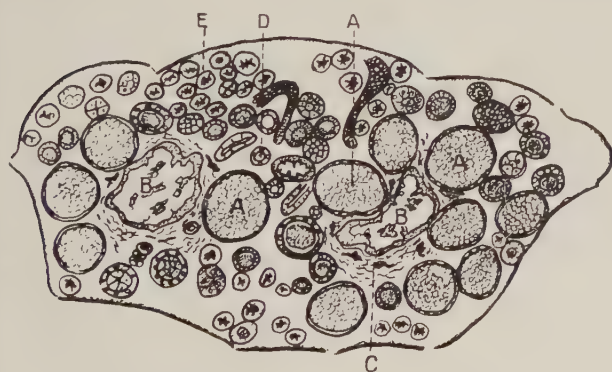


Abb. 4. — Querschnitt durch das Abdomen eines physogasteren *Anergates* ♀, vereinfacht.

Vergr. 25 fach.

A = Oocyten, B = Oviduct, C = Hüllgewebe um die Ovidukte, D = Malpighigefäß, E = Fettzellen.

sind sie am gewaltigen Anschwellen des Abdomens zu erkennen (= Physogastrie). MERGELSBERG (1934) unterscheidet elastisch-passive Körperveränderungen ohne histologische Neubildungen und plastische Dehnungsprozesse mit irreversiblen Veränderungen der Körperform und histologischen Neudifferenzierungen. Es kann keinem Zweifel unterliegen, daß *Anergates*

zur zweiten Gruppe gerechnet werden muß. Ebenso zählen hierzu *Tunga penetrans* (GEIGY und HERBIG, 1949) und zahlreiche Termitoxenien.

Andere Ameisen, z. B. *Lasius niger*-♀♀, werden während des Höhepunktes der Eiproduktion im Frühjahr vorübergehend reversibel physogaster, bedingt durch die Hypertrophie der Ovarien.

Auch bei *Anergates* sind in erster Linie die gewaltig hypertrophierten Ovarien für die Physogastrie verantwortlich. Synchron mit deren Wachstum verläuft offensichtlich ein irreversibles Wachstum sämtlicher anderer Organe der Ameise. Leider ist es bis jetzt noch nie gelungen, *Anergates*-♀♀ vom Ausgangsstadium (stenogaster) bis zur vollentwickelten Physogastrie im Formicarium zu halten, so daß eine vergleichende Untersuchung von Zwischenstadien nicht möglich ist. Deshalb stößt eine Deutung für die Größenzunahme auf beträchtliche Schwierigkeiten. Seltsamerweise wird auch das ZNS um ungefähr das Doppelte vergrößert. Für dieses Gewebswachstum — mit Ausnahme des ZNS — sind wohl kaum Mitosen verantwortlich, viel näher liegt dagegen die Möglichkeit eines Gewebswachstums durch Polyploidisierung (Vergl. RISLER, 1954).

Auch die sehr stark beanspruchten Intersegmentalhäute werden verdickt und sind etwa doppelt so breit wie die Cuticula. Sie weisen eine horizontale Strukturierung und eine apikale dunkle Grenzschicht auf. Es kann also von der Ausbildung einer sekundären Cuticula gesprochen werden.

Das Epithel der Ovidukte wölbt sich in lappigen Fortsätzen in das Lumen. Außerdem sind die Ovidukte von einer Schicht von Fasern wahrscheinlich bindegewebiger Herkunft umgeben. Bei anderen Ameisen-♀♀ fand sich jetzt noch keine vergleichbare Erscheinung.

j) **Erörterung der Ergebnisse.** — Die zu erwartende Beziehung zwischen der Lebensweise und der Organisation trat besonders beim ♂ sehr deutlich hervor. So scheint bei seiner Muskulatur eine weitere Rückbildung biologisch nicht mehr tragbar. Ebenso degenerierten Teile des Darmtraktes. Am auffallendsten hat sich der Verlust sozialer Instinkte ausgewirkt. Die Herabsetzung des Gehirnvolumens, besonders auf Kosten der assoziativ tätigen Zentren, steht unter den Formiciden wohl einmalig da. Dagegen ist das ♀ weit weniger degeneriert und somit zu seiner wesentlichsten biologischen Aufgabe, der Koloniegründung, befähigt. Seine Cuticula ist im Gegensatz zu der des ♂ die einer freilebenden Form, sein Flugvermögen bleibt erhalten, der Verdauungstraktus ist nicht degeneriert. Dagegen verschwand, da nicht mehr benötigt, der Stachelapparat vollständig, wenn wir nicht einige Drüsentubuli ohne Ausführungsgang in der Analgegend als rudimentäre Giftdrüse ansprechen wollen.

Eine weitere Anpassung des physogastren-♀ tritt uns in der postimaginalen Vergrößerung des Zellvolumens aller Somazellen entgegen. Abgesehen vom Nervensystem sind hierfür sehr wahrscheinlich Polyploidisierungsvorgänge verantwortlich zu machen. Die gewaltige Vergrößerung des Abdomens wurde erst durch die Ausbildung einer sekundären Cuticula (verhärtete und verdickte Intersegmentalhäute) möglich, da diese in ihrer ursprünglichen Form der Beanspruchung durch die Physogastrie auf die Dauer nicht gewachsen wären.

Die Ursache für das eifrige Belecken der *Anergates*-Geschlechtstiere, besonders der ♂♂, durch die *Tetramorium*-♀♀ konnte auf histologischem Wege nicht gefunden werden, da eine exkretorische Tätigkeit der Epidermis oder Trichome nicht nachzuweisen waren.

Die beim ♂ auftretenden Rückbildungsercheinungen lassen sich als Auswirkungen der frühzeitigen Geschlechtsreife verstehen. Durch die vorzeitige Entwicklung und Reife der Gonaden wird die weitere Differenzierung anderer Organe betroffen, und bleibt teilweise auf einem präimaginalen Stadium stehen.

Weitherhin werden Rückbildungen, wie sie besonders die ♂♂ aufweisen, durch die Aufsplitterung der Art in kleinste adelphogame Fortpflanzungsgemeinschaften gefördert und so eine Anreicherung degenerativer Anlagen ermöglicht. Beim *Anergates*-♂ kam es wahrscheinlich über richtungslose Mutationen u. a. zum Flügelverlust. Es können, durch Sozialparasitismus bedingt, Formen entstehen, die solitär nicht mehr lebensfähig wären und der Selektion zum Opfer fallen müßten. Im Schutze der sozialen Insektenstaaten ist ihre Existenz aber vorläufig gesichert. Durch die Isolierung wird ein Auftreten des nämlichen oder analogen Mutats begünstigt, wodurch eine Rückkehr zum ursprünglichen Typ absolut unwahrscheinlich wird (vergl. Kosswig, 1949). Es bestehen zweifellos Analogien zwischen der regressiven Evolution mancher Höhlentiere (Kosswig, 1949) und *Anergates*.

4. Zusammenfassung.

1. Beim ♂ von *Anergates* ist neben Teilen des Darmtraktes besonders die Skelettmuskulatur zurückgebildet. Das Gehirnvolumen wurde auf Kosten der assoziativen Zentren herabgesetzt. Der Bau des ♀ entspricht dem einer freilebenden Art, lediglich der Stachelapparat ist nicht mehr nachweisbar.

2. Postimaginal findet beim ♀ eine auffallende Vergrößerung aller Somazellen statt, für die — mit Ausnahme des Nervensystems — Polyploidisierungsvorgänge verantwortlich sind. Zur Festigung des Exoskeletts verhärteten die Intersegmentalhäute.

3. Als Folge der Isolierung von *Anergates* sind gewisse Analogien zur regressiven Evolution mancher Höhlentiere festzustellen.

Summary.

1. The male of *Anergates* shows a reduction of some parts of the digestive system and the musculature of the skeleton. The volume of the brain is reduced by reduction of association centres. The anatomy of the female corresponds to a free-living species, only the stinging apparatus cannot be found.

2. During the reproductive phase a remarkable enlargement of all somatic cells takes place due to polyploidy with exception of the nervous system. To strengthen the exoskeleton the intersegmental membranes are hardening.

3. As result of isolation of *Anergates* certain analogies to regressive evolution of some cave animals are noted.

Résumé.

1° Le mâle d'*Anergates* présente une réduction de la musculature squelettique et de quelques parties du tractus digestif. Le volume des ganglions cérébroïdes est diminué par suite de la réduction des centres d'association. L'anatomie de la femelle rappelle celle des femelles sauvages, à ceci près que l'aiguillon et ses annexes sont absents.

2° A part les cellules nerveuses, toutes les cellules somatiques de l'imago subissent une croissance remarquable à cause de leur polyploidie. Les membranes intersegmentales se durcissent et renforcent l'exosquelette.

3° Eu égard à l'isolement d'*Anergates*, on peut constater certaines analogies entre les phénomènes régressifs qu'il présente et ceux rencontrés chez des animaux cavernicoles.

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FACTEURS DU MILIEU AGISSANT SUR L'ACTIVITÉ DES COLONNES DE RÉCOLTE CHEZ LA FOURMI *Cremastogaster scutellaris* Ol. (Hymenoptera, Formicoidea)

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Les colonnes de récolte formées par les ouvrières de *Cremastogaster scutellaris* sont des formations très stables, au moins pendant une saison. Les colonnes empruntent des pistes strictement définies et permanentes (on peut démontrer, par des expériences de destruction partielle des pistes et en observant leur reconstitution, que les ouvrières utilisent uniquement des repères olfactifs). En choisissant un nid de *Cremastogaster scutellaris* ne possédant qu'une seule piste menant vers le champ trophoporique, on peut estimer avoir une idée de l'activité des ouvrières hors du nid en étudiant simplement le comportement de la colonne empruntant cette piste unique. Il est possible, en établissant une méthode de comptage des ouvrières en un point de cette colonne, d'établir une série de chiffres-indices qui exprimeront l'activité de la colonne et, par suite, l'activité des ouvrières hors du nid. Par exemple, le maximum d'activité de la colonne est mesuré par le chiffre le plus élevé qui indique le plus grand nombre moyen de passages devant un repère, dans l'unité de temps choisie. De même, le minimum d'activité est mesuré par l'indice le plus faible.

On peut alors, en se servant de la variation de ces indices en fonction des différents facteurs du milieu, étudier l'action de ces facteurs sur l'activité des ouvrières.

Le facteur principal agissant sur l'activité des colonnes est la température. Nous avons examiné aussi l'action du degré hygrométrique de l'air ambiant et l'action de la lumière.

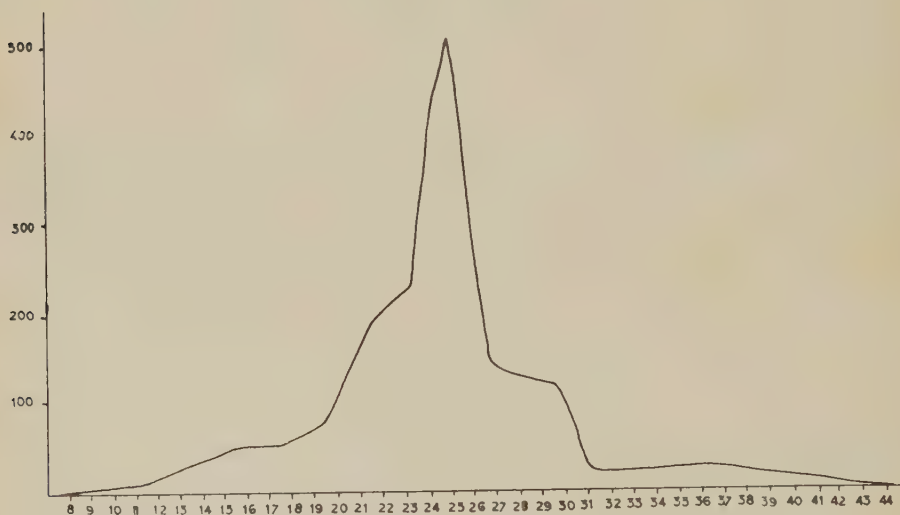
1^o ACTION DE LA TEMPÉRATURE. — Les observations dans la nature et les essais expérimentaux montrent l'existence d'un thermo-préférendum situé aux environs de 25° C. pour lequel l'activité de la colonne est maxima. Quand la température s'abaisse au-dessous de 25°, l'activité décroît rapidement et, au-dessous de 7°, il n'y a plus d'ouvrières circulant

sur la piste. Quand la température monte au-dessus de 25° , l'activité décroît encore plus vite et, à 44° , on peut considérer qu'il y a inactivité totale sur la piste.

Sur un nid en observation, nous avons relevé les moyennes suivantes pour les années 1953 et 1954 (périodes d'été).

Le premier des chiffres entre tirets indique la température et le deuxième est le chiffre-indice mesurant l'activité de la colonne.

— $7^{\circ} : 0$ — $11^{\circ} : 3$ — $13^{\circ}, 14^{\circ} : 27$ — $15^{\circ}, 16^{\circ} : 50$ — $17^{\circ}, 18^{\circ} : 53$ — $19^{\circ}, 20^{\circ} : 81$ — $21^{\circ}, 22^{\circ} : 191$ — $23^{\circ}, 24^{\circ} : 228$ — $25^{\circ} : 501$ — $26^{\circ}, 27^{\circ} : 142$ — $29^{\circ}, 30^{\circ} : 123$ — $31^{\circ} : 21$ — $36^{\circ}, 37^{\circ} : 26$ — $40^{\circ} : 13$ — $44^{\circ} : 1$.



COURBE N° 1.

En abscisses : températures en degrés.

En ordonnées : chiffres-indices mesurant l'activité de la colonne.

En approfondissant l'examen des chiffres-indices, on s'aperçoit que l'accroissement d'activité le plus intense a lieu pour des températures allant de 22° environ à 25° , et la diminution d'activité la plus rapide pour des températures comprises entre 26° et 27° .

2° ACTION DU DEGRÉ HYGROMÉTRIQUE DE L'AIR AMBIANT. — Nous n'avons pu mettre en évidence une action indépendante de ce degré hygrométrique. Cette action, si elle existe, est si faible qu'elle est masquée par celle de la température.

En revanche, l'influence des précipitations (rosée et surtout pluie) est très nette. C'est d'ailleurs une simple action mécanique, qui entraîne

temporairement des perturbations profondes dans l'activité de la colonne, pouvant aller jusqu'à l'interruption totale de celle-ci.

3^o ACTION DE LA LUMIÈRE. — La lumière n'exerce aucune action sur l'activité de la colonne. Les observations ont été faites de jour comme de nuit et les modifications dans l'activité de la colonne ne sont dues qu'aux variations de la température.

On peut donc admettre que l'activité des colonnes d'ouvrières de *Cremastogaster scutellaris* ne dépend, parmi les facteurs étudiés, que du facteur température. Il existe, pour cette espèce, un thermo-préférendum pour lequel l'activité des colonnes est maxima : il se situe aux environs de 25°. Au-dessous de 7° et au-dessus de 44°, l'activité des colonnes est pratiquement nulle.

En fonction de ces résultats, il est intéressant d'étudier les variations journalières de l'activité des colonnes de récolte.

PARCK (1935) a signalé que l'activité des fourmis est arythmique ; CHAUVIN (1944) vérifie ces constatations chez *Leptothorax tuberum* var. *corticalis* et déclare que les ouvrières isolées ou en petit groupe ne présentent aucun rythme nycthémeral bien défini. REICHLE (1943), sur différentes espèces de *Myrmica*, constate que l'activité est arythmique et relève, dans l'activité des vingt-quatre heures, l'existence de deux maxima, indépendants de l'offre ou de la prise de nourriture, mais directement liés à la température ou à l'humidité.

Chez *Cremastogaster scutellaris*, nous avons étudié l'activité collective journalière, c'est-à-dire l'activité des colonnes de récolte dans leur ensemble et dans des conditions naturelles, et non plus l'activité d'ouvrières isolées ou constituées en petits groupes expérimentaux. Cette activité collective est sous la dépendance directe et prépondérante de la température. La courbe retraçant l'activité journalière est établie au moyen des chiffres-indices d'activité. La forme de cette courbe s'explique par l'existence (signalée dans la première partie de cette note) d'un thermo-préférendum pour lequel l'activité de la colonne est maxima.

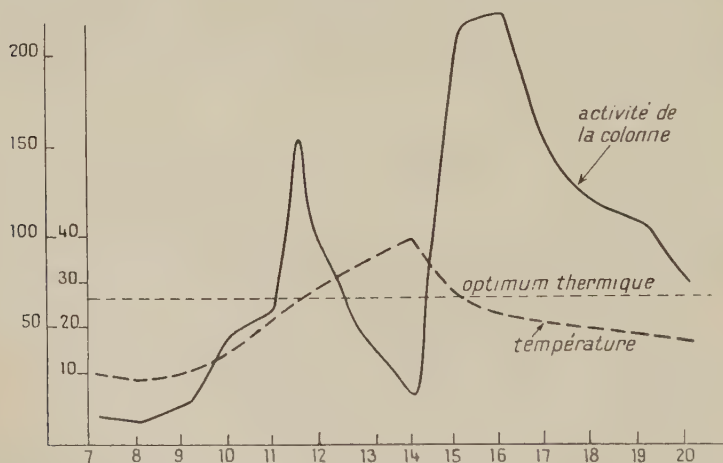
Si, dans une journée, la température s'élève au delà de l'optimum de température qui est de 25° pour cette espèce, l'activité passe par un premier maximum correspondant au thermo-préférendum. Puis cette activité décroît au fur et à mesure que la température s'élève au-dessus de l'optimum. Par la suite, la courbe des températures s'abaissant, l'activité atteint un deuxième maximum (qui correspond à un nouveau passage des températures par l'optimum thermique), et enfin l'activité se ralentit en fonction de la température quand celle-ci descend au-dessous de l'optimum.

Dans nos régions, il n'y a jamais passage des températures à 25° pendant la nuit et les maxima d'activité ne se manifestent donc que pendant la journée.

OBSERVATION DU 1^{er} OCTOBRE 1953.

Heures.	Températures.	Chiffres-indices.
7 h. 20	11°,5	4
7 h. 35	11°,5	4
8 heures	10°,8	2
9 —	13°	13
10 —	16°	50
11 —	22°,5	58
11 h. 35	25°,5	159
12 heures	30°	103
13 —	36°,5	46
14 —	40°	13
15 —	26°,5	217
16 —	24°	223
17 —	22°,5	145
18 —	20°	118
19 —	19°	112
20 —	17°	75

Les indications de ce tableau ont permis de construire la courbe n° 2.



COURBE N° 2.

En abscisses communes : heures de la journée.

En ordonnées de la courbe des températures : températures en degrés.

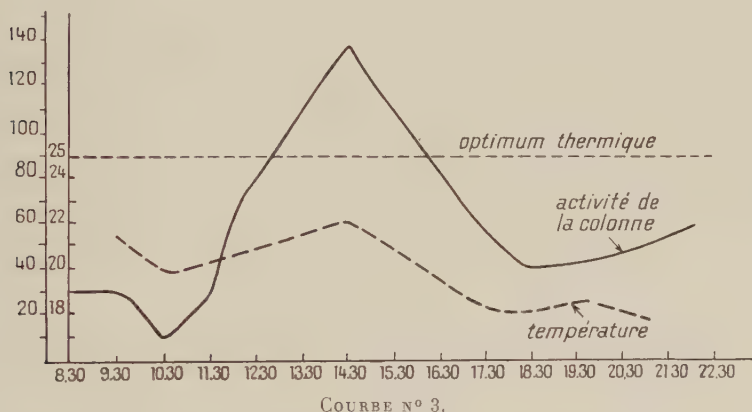
En ordonnées de la courbe d'activité : chiffres-indices d'activité.

Mais il arrive que la température maxima des vingt-quatre heures corresponde à l'optimum thermique ou soit légèrement inférieure. Dans ce cas-là, nous n'aurons qu'un seul maximum d'activité : au moment du passage des températures par le thermo-préférendum ou par le point qui en est le plus proche.

Les indications du tableau suivant ont permis de construire la courbe n° 3.

OBSERVATION DU 13 OCTOBRE 1953.

Heures.	Températures.	Chiffres-indices.
8 h. 35	21°,5	30
9 h. 30	21°,5	30
10 h. 30	20°	9 (pluie) ¹
11 h. 30	20°,5	38
12 heures	21°	61
14 h. 30	22°	137
17 h. 30	19°	57
18 h. 30	18°,5	40
20 h. 30	18°,7	45 (nuit)
22 heures	18°	58 (nuit) ²



COURBE N° 3.

En abscisses communes : heures de la journée.

En ordonnées de la courbe des températures : températures en degrés.

En ordonnées de la courbe d'activité : chiffres-indices d'activité.

Nous retrouvons donc les conclusions de REICHLÉ en remarquant seulement que l'existence de deux maxima d'activité dans les vingt-quatre heures n'est, chez *Cremastogaster scutellaris*, qu'un cas particulier de l'action directe de la température, puisque, dans certains cas, il peut n'y avoir qu'un seul maximum d'activité par vingt-quatre heures.

Nous pouvons donc conclure que :

1° Dans les colonnes de *Cremastogaster scutellaris*, l'activité est arythmique.

2° Les maxima d'activité journalière sont déterminés par le passage de la température par un optimum thermique.

(1) Ce chiffre anormalement bas indique de façon très nette l'influence considérable que les précipitations exercent sur l'activité de la colonne, ainsi que cela est signalé dans la première partie de cette note.

(2) L'approche brutale d'une vive lumière pour permettre de compter les fourmis circulant sur la piste a entraîné des perturbations dans le comportement des ouvrières ; beaucoup ont fait demi-tour à une certaine distance du repère de comptage et, de ce fait, ont été comptées deux fois.

II

NOUVELLES DE L'UNION

TRAVAUX PUBLIÉS PAR LES MEMBRES DE L'UNION

1942. BECKER (G.), SCHULZE (B.), SCHULZ (E.). — Prüfung der vorbeugenden Wirkung von Holzschutzmitteln gegen Termiten (*Wiss. Abh. Dtsch. Materialprüfungsanst.*, II, 3, 40-55).
1946. BECKER (G.), SOMMER (H.). — Ueber die Berücksichtigung der Gebrauchseinflüsse bei der Prüfung von Textilien mit Sonderausrüstung auf Termitenfestigkeit (*Melliand Textilberichte*, 27, 247-251).
1954. BECKER (G.), THEDEN (G.). — Jahresberichte über Holzschutz. Annual Report on Wood Protection 1951-1952. Berlin.
1942. BECKER (G.). — Der Einfluß verschiedener Versuchsbedingungen bei der « Termitenprüfung » von Holzschutzmitteln unter Verwendung von *Calotermes flavicollis* als Versuchstier (*Wiss. Abh. Dtsch. Materialprüfungsanst.*, II, 3, 55-66). — 1942. Prüfung von Textilien auf « Termitenfestigkeit » (*Melliand Textilberichte*, 23, 523-527 u. 573-577). — 1948. Ueber Kastenbildung und Umwelteinfluß bei Termiten (*Biolog. Zbl.*, 67, 407-444). — 1950. Prüfung der « Tropeneignung » von Holzschutzmitteln gegen Termiten (*Wiss. Abh. Dtsch. Materialprüfungsanst.*, II, 7, 62-76). — 1950. Zerstörung des Holzes durch Tiere. In : Mahlke-Troschel-Liese, *Handbuch der Holzkonservierung*. 3. Aufl., Berlin (J. Springer), 111-165. — 1951. Ueber einige Ergebnisse und Probleme der angewandten Entomologie auf dem Holzschutzgebiet (*Verh. Dtsch. Ges. angew. Entomol. e. V.*, 47-70). — 1952. Beobachtung der Kopulation bei *Calotermes flavicollis* Fabr. (Isoptera) (*Zool. Anz.*, 148, 270-273). — 1952. Untersuchungen über die Schutzwirkung von Pentachlorphenol gegen holzerstörende Insekten (*Holz als Roh- u. Werkstoff*, 10, 341-352). — 1953. Einige Beobachtungen über holzerstörende Insekten (Termiten und Käfer) in Guatemala (*Z. angew. Entomol.*, 35, 339-373).
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NOTES ET ANALYSES

THOMAS E. SNYDER. — **Order Isoptera — The Termites of the United States and Canada**, 64 pp. Illustrated (*Technical Bulletin Published by National Pest Control Assoc.*) New-York, 1954.

This compact book is a timely and needed summary of the main characteristics and habits of the 41 species known in the area. Practical keys to both winged forms and soldiers are provided. The publication is obviously intended for the use of pest control operators and its arrangement and contents should be a useful and ready reference for the conscientious members of that industry as well as for general entomologists.

The species described are conveniently tabulated taxonomically and geographically by states; a glossary of technical terms is included. Twenty-nine illustrations aid the novice in visualizing actual contrasts in related forms, although in this reviewer's opinion the variability in scale amongst figures that often need to be compared lessens the usefulness of these illustrations. Very few typographical errors were noted; the text is clean. Brief instructions on the preservation and handling of specimens for identification would have been useful. The last half of the publication is devoted to the habits and elementary ecology of the 41 species—a field in which Dr. SNYDER writes with an authority born of long experience.

E. Morton MILLER.

Published in France.

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Dépôt légal 1955 - 2^e trimestre - N^o d'ordre : 2140 - MASSON et C^{ie}, éditeurs, Paris.

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Dépôt légal 1955 - 2^e trimestre - N^o d'ordre 6102.

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